UNIVERSITÀ DEGLI STUDI DI NAPOLI FEDERICO II

THE PLIO-HOLOCENE LARGE MAMMALS OF THE WESTERN EURASIA: MACROECOLOGICAL AND EVOLUTIONARY ANALYSES OF THE FAUNAS

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To Daniela and my family

“The most erroneous stories are those we think we knowbest - and therefore never scrutinize or question.”

Stephen J. Gould

Index

Preface

The climate during the Plio-Pleistocene was deeply influenced by the so called Milankovitch cycles (Zachos et al.,2001). These are combinations of different astronomical phenomena involving the variation of the Earth's orbital eccentricity, the axis obliquity and precession. The first phenomenon was estimated to occur every 400-100 Ka, whereas the others occur over a time period of 41 and 23-19 Ka, respectively. These astronomical variations influenced the Earth-Sun distance and the angular incidence of solar rays with a net effect on the global climate change (Zachos et al., 2001).

The Early Pliocene was characterized by a decrease of the global temperature, a trend that began during the Late Miocene. The measure of the mean $^{16}O/^{18}O$ values indicates a trend of warmer climate until 3.2 Mya, the latter that represents the onset of a new temperature cycle. During these cycles the ice sheet expanded and contracted according to the variation of the mean global temperature. Indeed, in the Middle Pliocene, the ice sheets began to cover the Northern Hemisphere, an event indicated as NHG (North Hemisphere Glaciation) (Shackleton et al., 1998; Maslin et al., 1998; Zachos et al., 2001).

At ~2.5 Mya the oscillations of the temperature became quite a regular pattern determining the alternation between warmer (Interglacials) and cooler (Glacials) time periods, that were to characterize the Pleistocene.

Some 1 May (period coincident with the Jaramillo Event of Earth's Magnetic Field inversion) the time interval of a complete climatic cycle changed its duration from the 41-23-19 Kya., to a new longer cycle of 100 Kya, probably determined Earth's orbital eccentricity variation. With the increase of the duration of the cycles the mean global temperatures reached more extreme values and there were stronger climate ranges between warm and cold periods. Moreover, the measures of the oxygen isotopes ratios confirm a net decrement of mean temperature values recorded from the Late Pliocene to the Recent (Zachos et al., 2001).

The strong oscillations of the temperatures during the Plio-Pleistocene deeply influenced the faunas of the whole world. These environmental changes determined local or mass extinctions in some cases or migration events in other cases (Lister, 2004). In particular, during the Glacials, the species adapted to warmer climates

migrated southward, while, during the Interglacials, the species adapted to low temperatures migrated northward (Vrba, 1995b). There are many demonstrations of the influence of the climate changes on the evolution of mammals faunas, also at the community level (Vrba, 1995a,b; Alroy et al., 2000; Fortelius et al., 2002, 2006; Barnosky et al., 2003; Bobe and Behrensmeyer, 2004; Rodríguez et al., 2004; Raia et al., 2005; Barnosky and Kraatz, 2007; Meloro et al, 2008).

Starting from these considerations on the evolution of mammal faunas, the aims of this doctoral thesis were focused on the detection of the paleocommunities of large mammals that lived since the Late Pliocene to the Early Holocene in the Western Eurasia and on their macroecological investigations in the light of climatic change. After collecting a great deal of data (811 Local Faunal Assemblages, LFA, and 220 large mammal species) the paleocommunities (here called EA PCOM) were detected using new statistical methods that avoid any subjective criteria in selecting the LFAs. Moreover, considering two recent articles (Alroy, 2000; Fortelius et al., 2006) a statistical-based time ordination of the collected fossil localities was obtained.

As for their well defined temporal and geographical resolution, the EA PCOMs were discussed from the point of view of the distribution of the included LFAs. These analyses showed the presence of both spatial and temporal patterns, useful for inferring dispersal events of mammals in response to the environmental changes. From this point of view, EA PCOMs provide a paleontological framework for evolutionary and ecological investigations.

All the collected LFAs were then used to perform statistical analyses to detect macroecological patterns that usually characterize the living mammal assemblages. At first, there were the reconstruction of the body masses and of the duration of both species and genera of the considered taxa. Then, the fossil mammal faunas were investigated to draw the occupancy and the range size trajectories over taxa life span, both at the species level and at the genera level. To this aim the occupancies and the range sizes were computed in different moment of taxon life time. Further, the data provided by occupancy and range size values were used to draw general models that decribe the most frequent coarses in both species and genera time life span. Some other statistics were computed over occupancy, range size and body size and, then, used to infer on their possible influences on the taxon duration. In addition, the data of the species occurrences were used to build the species-time, the species-area and the

species-time-area relationship (STAR), that are all patterns typically recognized in living species. Moreover, the latter model (the STAR) was investigated for the first time in fossil species.

The interdisciplinary approach of this doctoral thesis also involved the use of modern phylogenetic techniques to seek any relationships in all the measured traits between closely related taxa. To this aim, the phylogenetic trees of all the considered species and genera were reconstructed using data provided by genetic, morphologic and evolutionary studies. A second step was to combine the phylogenetic trees and all the other computed measures to infer about the models of evolution followed by the traits characterizing the large fossil mammals.

All the computed results were used to draw possible evolutionary scenarios concerning the Plio-Pleistocene mammal faunas.

Chapter 1 - The Eurasian Paleocommunities

1.1 Introduction

The past investigations on fossil mammal assemblages showed striking examples of evolutionary changes during the Quaternary. The results coming from these studies arose the supposition of a direct link between the acceleration of the evolution of mammals and strong the environmental changes recorded for the Ice Age (Lister, 2004). For years the available tool for vertebrate palaeontologists to detect fossil mammal assemblages and to perform macroecological hypothesis testing was constituted by biochronological schemes such as European MN zones (Mein, 1975) and North American NALMAs (Wood et al., 1941; Woodburne and Swisher, 1995). These systems are based on the grouping of Local Faunal Assemblages (LFAs) defined by the occurrences of particular key species. For example, when the Committee with E. Wood as chairman created for the first time the Land Mammal Ages, it was probably influenced by the article of R.A. Stirton (1936) in which the author divided the Pliocene in three parts based on the assemblages of mammals. These latter were characterized by first appearance and last appearance of well represented taxa (primarily horses). The Land Mammal Ages are biochronologic units defined as a relatively short interval of geologic time that can be recognized and distinguished from earlier and later such units by a characterizing assemblages of mammals (Lindsay, 2003).

Some authors (Caloi and Palombo, 1998; Sardella et al., 1998; Petronio and Sardella, 1999; Palombo et al., 2003; Rodriguez et al., 2004) considered the organization of Mammal Ages restricted to the Italian peninsula as useful tool for studying the ecological patterns of the Quaternary mammal communities in response to the climate changes characterizing that temporal interval. But, as already, the boundaries of a Biochron (Williams, 1901) are defined by the First Appearance Datum and Last Apperance Datum of particular taxa (Lindsay, 2003). The datum event concept was developed by Bandy (Bandy, 1963a, 1963b, 1964) for biostratigraphic markers in planktonic foraminifera found in the marine deposits. These markers have the characteristics to be widespread and near contemporaneous in their distribution in deep-water deposits (Lindsay, 2003). Unfortunately the terrestrial records are discontinuous and fossils are often rare due to taphonomic biases (Raia et al., 2006). In

this regards the use of Biochrons is not the best solution to detect fossil communities of terrestrial vertebrates. Also the definition of "community" (McIntosh, 1995) was coined for living organisms and its application to fossil organisms is quite misleading. Moreover palaeontologist have to face off with the time factor that introduces a new dimension in any kind of possible definition of a fossil community. Thereby the method to recognize mammal communities is critical for investigating their evolution (Raia et al., 2006). In this chapter I will apply a recent statistical technique called Bootstrapped Cluster Analysis applies to the Western Eurasian Local Faunal Assemblages of fossil large mammals of the Plio-Holocene. This method allowed the detection of Eurasian fossil communities. To this aim the following procedures were applied:

- The collection of the Local Faunal Assemblages (LFAs) of Western Eurasia large mammals spanning in time from the Middle Pliocene to the Early Holocene.
- The creation of a presence/absence matrix using the fossil occurrences data.
- The computation of a temporal ordination of the LFAs based on statistical methods and that is independent of radiometric and paleomagnetic age estimates
- The detection Eurasian paleoccommunities (EA PCOM) by statistical methods and the setting of their spatial and temporal boundaries.

1.1.1 The italian Paleocommunities (PCOMs)

In 2006, Raia et al. presented a paper in which they showed the detection of the Italian paleocommunities of the Plio-Quaternary large mammals. They started this project to provide palaeontologists a tool for the application of ecological studies to fossil mammals.

For the detection of the mammal communities they used a new statistical tool called Bootstrapped Cluster Analysis (BCA) (Pillar, 1999). Shortly, the BCA is a statistical tool useful to detect natural groupings of items also providing a probability value for any partition level identified. Thereby, the novelty in this new method is to free the results of the analyses from any subjective criteria. This was very useful to provide a definition for fossil communities as it doesn't suffer of the necessity to choose a-priori taxa characterizing the geographical and temporal boundaries. The Bootstrapped Cluster Analysis will be exhaustively described later, as it was employed for the aims of this

doctoral thesis too. As results of these analyses, Raia et al., 2006 obtained the detection of nine Italian paleocommunities, they called PCOMs (Table 1.1). They found 5 Villafranchian PCOMs, 3 Galerian PCOMs and 1 Aurelian PCOM. Their scheme partially alters the one proposed by Gliozzi et al. (1997) (Figure 1.1), as, for example, the beginning of the Galerian was usually identified by the arriving of *Praemegaceros verticornis,* but in the PCOM's scheme the locality that records the FO of this species, Collecurti, is included in a typically Villafranchian PCOM. The author explained that the interpretation of this incongruence is due by the fact that, probably, Collecurti, although containing the species that typically remarks the onset of Galerian, have a faunal list that is very similar to Late Villafranchian LFAs. It is important to say that PCOMs are built on the need to detect discrete faunal assemblages and, thereby, their temporal boundaries are determined by considerable changes in the assemblages. On this regards, authors pointed out that this is one of the most important reasons to state that PCOMs are not Biocronological units.

Clustering units			PCOMs	Local faunal assemblages LFAs
G3	G3.2		Aurelian	Bucine, Campo Verde, Casal de' Pazzi, Castel di Guido, Cerveteri, Contrada Monticelli, Fara Sabina, Grotta Romanelli, La Polledrara di Cecanibbio, Malagrotta, Monte delle Gioie, Grotta Paglicci, Pontecorvo, Prati Fiscali, Quisisana (Capri), Riano, Sedia del Diavolo, Torre In Pietra (lower beds), Torre In Pietra (upper beds), Torrente Conca, Vitinia (upper beds)
	G3.1	G3.1.3	Galerian 3	Cava Campani, Cava Nera Molinario, Fontana Ranuccio, Notarchirico, San Romano, Spessa 2, Venosa-Loreto, Visogliano
		G3.1.2	Galerian 2	Cesi, GRA, Isernia La Pineta, Valdemino
		G3.1.1	Galerian 1	Borgonuovo, Monte Oliveto, Monte Tenda, Pitigliano, Ponte Galeria 2, Slivia
G2	G2.4		Villafranchian 5	Capena, Colle Curti, Imola, Madonna della Strada, Pirro Nord, Redicicoli
	G2.3		Villafranchian 4	Il Crostolo, Mugello (fluviolacustrine), Pietrafitta, Selvella, Val di Chiana (Farneta)
	G2.2		Villafranchian 3	Bacino Tiberino (various sites), Casa Frata, Casa Sgherri (Massarella), Faella, Fontana Acetosa, Matassino, Monte Riccio, Olivola, Pantalla, Poggio Rosso, Torre di Picchio, Upper Valdarno (various sites)
	G2.1		Villafranchian 2	Cava Toppetti, Colle Pardo, Costa San Giacomo, Montopoli, Valle Catenaccio
G1			Villafranchian 1	Gaville, Triversa

Table 1.1 PCOMs and their Local Faunal Assemblages (LFAs)

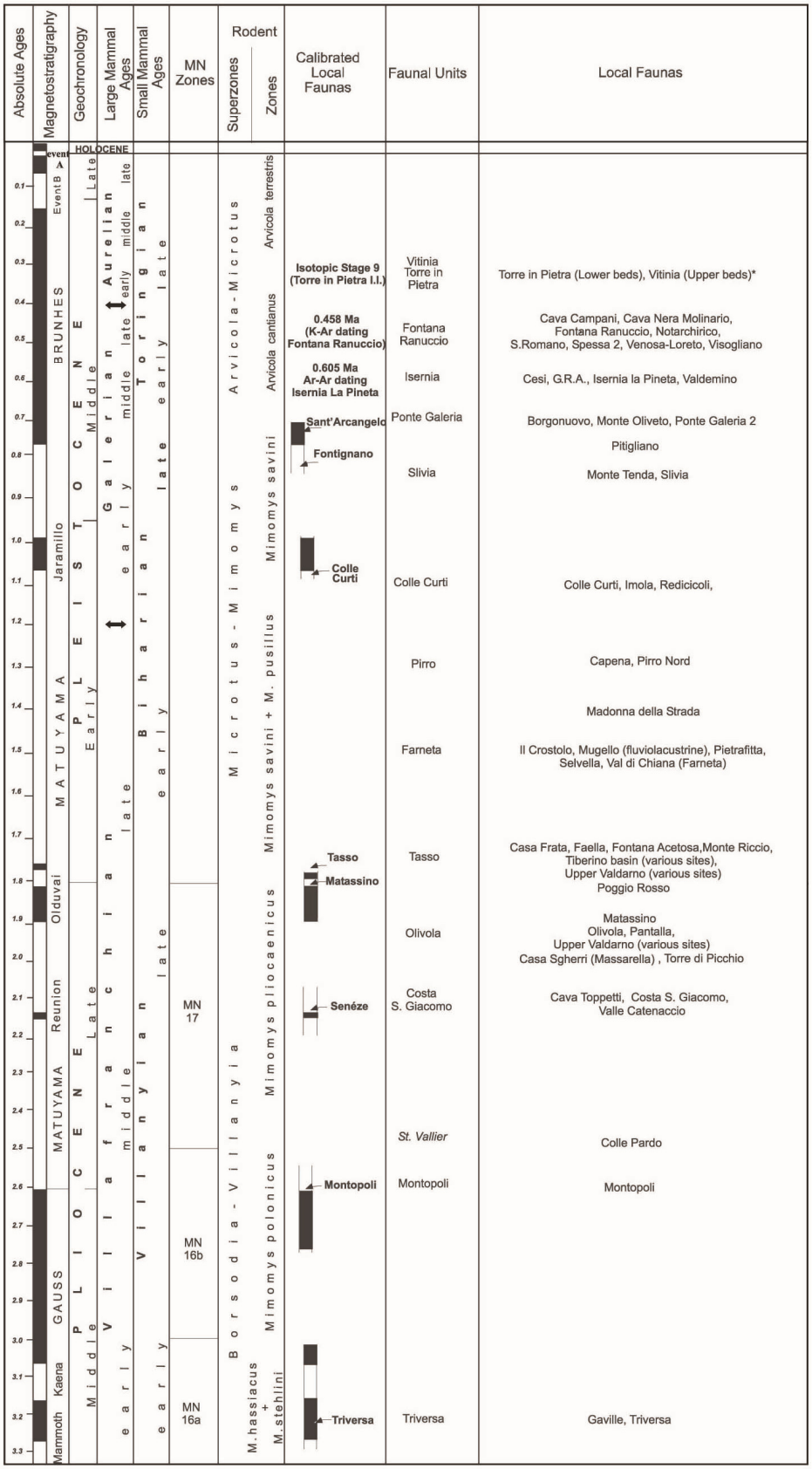

Absolute Ages
Magnetostratigraphy
Geochronology
Large Mammal Ages
Small Mammal Ages
MN Zones
Rodent
Superzones
Zones
Calibrated Local Faunas
Faunal Units
Local Faunas
HOLOCENE
Late
Middle
Early
PLEISTOCENE
PLIOCENE
BRUNHES
MATUYAMA
Jaramillo
Olduvai
Reunion
Kaena
Mammoth
GAUSS
Event A
Event B
Aurelian
Galerian
Villafranchian
Biharian
Toringian
Arvicola-Microtus
Microtus-Mimomys
Mimomys savini
Arvicola cantianus
Arvicola terrestris
Mimomys savini + M. pusillus
Borsodia-Villanyia
Mimomys pliocaenicus
Mimomys polonicus
M.hassiacus + M.stehlini
MN 17
MN 16b
MN 16a
Isotopic Stage 9 (Torre in Pietra I.l.)
0.458 Ma (K-Ar dating Fontana Ranuccio)
0.605 Ma Ar-Ar dating Isernia La Pineta
Sant'Arcangelo
Fontignano
Colle Curti
Tasso
Matassino
Senéze
Montopoli
Triversa
Vitinia Torre in Pietra
Fontana Ranuccio
Isernia
Ponte Galeria
Slivia
Colle Curti
Pirro
Farneta
Tasso
Olivola
Costa S. Giacomo
St. Vallier
Montopoli
Triversa
Torre in Pietra (Lower beds), Vitinia (Upper beds)*
Cava Campani, Cava Nera Molinario, Fontana Ranuccio, Notarchirico, S.Romano, Spessa 2, Venosa-Loreto, Visogliano
Cesi, G.R.A., Isernia la Pineta, Valdemino
Borgonuovo, Monte Oliveto, Ponte Galeria 2
Pitigliano
Monte Tenda, Slivia
Colle Curti, Imola, Redicicoli,
Capena, Pirro Nord
Madonna della Strada
Il Crostolo, Mugello (fluviolacustrine), Pietrafitta, Selvella, Val di Chiana (Farneta)
Casa Frata, Faella, Fontana Acetosa,Monte Riccio, Tiberino basin (various sites), Upper Valdarno (various sites) Poggio Rosso
Matassino
Olivola, Pantalla, Upper Valdarno (various sites) Casa Sgherri (Massarella) , Torre di Picchio
Cava Toppetti, Costa S. Giacomo, Valle Catenaccio
Colle Pardo
Montopoli
Gaville, Triversa

Figure 1.1

1.1.2 The properties of the Italian Paleocommunities: Body size and occupancy

Some following studies were focused on the ecological investigation of the Italian paleoccommunities. At first, the analyses concerned about the testing any similarities in the distribution of body size frequency between PCOMs and living mammal communities.

An exhaustive dissertation on frequency and geographical distribution of the body sizes will be provided in the second chapter of these doctoral thesis. Then, I will discuss only some concepts here just to introduce to the analyses performed on Italian paleocommunities.

The frequency distribution of body size varies according to the geographical scale of the sampling area (Gaston and Blackburn, 2000). Irrespective of the taxa considered, this distribution is log normal at smaller geographical scale, whereas it is strongly right-skewed at larger scales. One reason for this differences could be ascribed to a strong sampling bias at different geographical scale, but a frequently accounted explanation was given by MacArthur in 1959, according to which these patterns are due to the strong negative influence of habitat heterogeneity on smaller species. Indeed, small sampling areas includes few habitats then there are few small species. Considering larger sampling areas, more habitat are sampled and, then, there is an increase in the number of small species detected. The analyses conducted on Italian paleocommunities (Raia's doctoral thesis, 2003) depicted a body size distribution that is very similar to living communities of comparable geographical scale. Nevertheless, preliminary analyses showed that the body sizes of italian fossil mammals had a log normal frequency distribution that was in contrast to the expected result of a right-skewed distribution. Raia justified his results stating that the model drown for living species is built including small species too. Instead, in his project he excluded smaller taxa such as hares, rabbits, most primates, badgers, raccoon dogs, hedgehogs, porcupines, anteaters, wolverine, otters and most rodents. Indeed, he demonstrated that the body sizes of all these taxa represent the portion of measures that constitute the missing part of the pattern he detected.

The same project focused on the detection of possible evolutionary pattern in the temporal and geographical distribution of body sized of Italian fossil mammals. According to the Bergmann's Rule, different races within warm-blooded species are readily distinguished basing on their size, the largest living at higher latitudes

(Bergmann, 1847). The most accounted possible explanations of these rule are ascribed to the ability of larger taxa to survive in cold habitats as for their lower metabolic rate per unit body weight (McNab, 1971; Calder, 1996; West et al., 1997; Brown and West, 2000) and for their lower mass-specific heat loss (Calder, 1996). Then, Raia performed statistical analyses to test if such a pattern is shown by the taxa that lived in progressively colder habitats due to the climate trend characterizing the Quaternary. The results obtained showed no statistically significant pattern for the group considered (Artiodactyls, Perissodactyls and Carnivores). Instead, the patter was clear and significant at the community level when the Galerian and Aurelian PCOMs were considered. The latter result showed that in some ways, the large mammals occurred in Quaternary PCOMs, underwent an increase in their body sizes, probably ascribed to the trend of global cooling that started with the onset of the Galerian.

PCOMs were analyzed by the point of view of species occupancy too. In 2006, Raia et al., showed the results concerning the trajectories and the frequency distribution of species occupancy. The Italian paleocommunities showed both bimodal and unimodal-rigth-skewed frequency distributions, resembling living communities in the pattern predicted by Raunkiaer's law. Moreover, the most frequent occupancy trajectories had a peaked course as it occurs for the most living taxa (an exhaustive discussion on occupancy and its properties for living and fossil mammals will be provided in the second chapter of this doctoral thesis).

1.1.3 Species turnover, diversity trends, and prey-predator relationship

Another important investigation that involved the PCOMs was the detection of species turnover rates. The authors (Raia et al., 2005) used the groups of LFAs identified by the Boostrapped Cluster Analysis to compute turnover rates at the geographical scale of Quaternary Italian fossil paleocommunities. The project was lead to test if at the level of PCOMs and Faunal Units, the computed turnover rates are a consequence of the Red Queen Hypothesis (Val Valen, 1973) or are dominated by the climate changes as supposed in Vrba, 1995a,b. According to the first hypothesis, the turnover rates are constant during time intervals and are dominated by the ecological interactions between species, whereas, according to the point of view of Vrba, turnovers rapidly increase (pulses) in intensity in response to strong climate change that determines the

taxonomical changes of the communities. Actually, there is the belief that both the processes can influence the species' turnover, but at different geographical scales (Barnosky, 2001). At local scales, the ecological interactions have a major role in shaping the taxonomical composition of a community. At larger (continental) scales the ecological interaction give away to the climatic or tectonic factors.

For the computation of the turnovers a new technique was provided. This method was called transversal turnover rate (TVR) as it allows to compute turnover by considering the LO (Last Occurrence) and FO (First Occurrence) between two successive PCOMs or FUs.

The results of this study emphasized the turnovers computed at the onset of the Late Villafranchian, Galerian and Aurelian along with the relative computed PCOMs. This determined that the rates were more marked at the time period of stronger climate changes. The authors also performed statistical test to detect any kind of correlation between TVRs and climate changes (represented by the oxygen isotope standard residuals). The results of this latter test (Figure 1.2) reinforced the role of the climate on the more marked changes in the taxonomical composition of the paleocommunities.

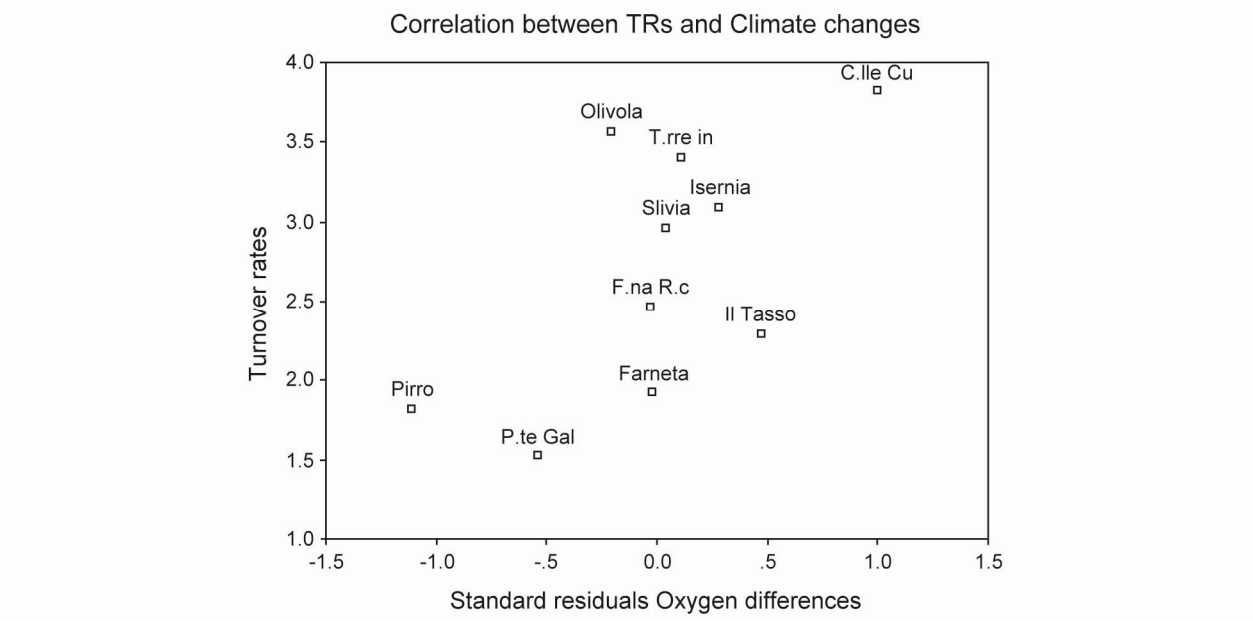


Figure. 1.2

In 2007, PCOMs were investigated from a point of view that was more ecological than macroecological or biogeographical. Indeed, in Raia et al. (2007) the computation and the variation through PCOMs of the predator-prey occurrence ratio (PPR) was performed.

A formerly study (Arnold, 1972) suggested the number of predators should follow the nomber of preys determining a costant ratio through time. Discordant evidences report this ratio to be both costant (Cohen, 1977; Jeffries and Lawton, 1985; Sugihara et al., 1989; Shoenly et al., 1991; Gaston et al., 1992; Warren and Gaston, 1992) or incostant (Simberloff, 1976; Valentine et al., 2002), thereby this question is still unresolved (Rosenzweig, 1995; Spencer et al., 1999; Croft, 2006). In Raia et al., 2007, the PPR was computed for each PCOM and then its variation was investigated testing if the variation in both predator and prey body sizes had affected its absolute values. In keeping with the consideration in Van Valkenburgh (1988), the authors considered any land carnivore larger than 10 kg to be a large predator. They excluded Cave bears (*Ursus spelaeus* and its very close relative *U. deningeri*) because isotopic analyses of dental enamel had indicated they fed exclusively on plant material (Stiner et al., 1998). They considered as “prey” mammals belonging to the orders Artiodactyla, Perissodactyla and Proboscidea. Small mammals vere excluded too according to Van Valkenburgh and Janis (1993) as large carnivores usually feed on prey as large as and even larger than themselves (Gittleman, 1985; Vezina, 1985; Carbone et al., 1999). Then they computed the body sizes of the selected taxa by applying regression equations published in Damuth and MacFadden (1990), Alberdi et al. (1995), and Christiansen (2004) The Figure1.3 shows the results of the PPR computation and its variation between PCOMS.

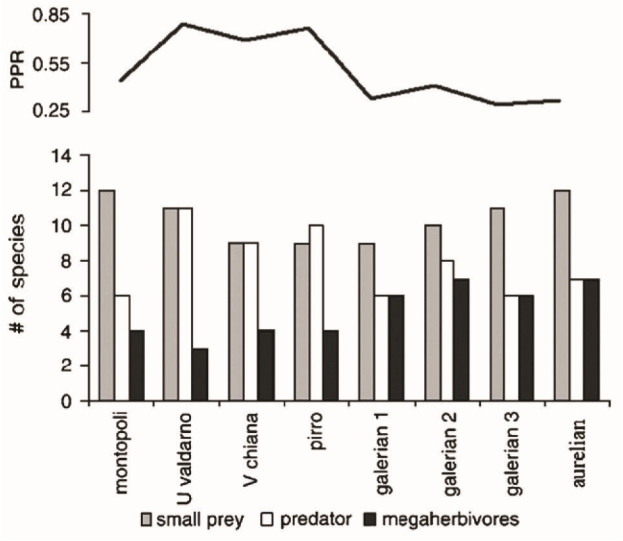


Figure 1.3 Predator/prey ratio (PPR) (solid line) compared with number of predators, number of smaller prey, number of megaherbivores (herbivores larger than 1000 kg, Owen Smith, 1990).

As it is possible to see, the PPR has two maximum values at a U Valdarno and Pirro PCOMS and then it decreases since Galerian 1 PCOM. The frequency distribution of body sizes per PCOM of both predators and prey shows that in the Villafranchian PCOMs there is the prevalence of small preys and predator, whereas in the Galerian-Aurelian PCOMs small preys are still the most abundant. Analyzing the general pattern it is possible to observe that small mammals decreased constantly reaching their lowest value at the Galerian 1 PCOM, then a new increasing trend started. As regards the predatros two maxima values are recorded at U Valdarno and Pirro and they conindes with the PPRs maxima. Then it is possible to observe a very interesting trend regarding the megaherbivores that costantly increase in abundance since the first PCOM and then equaling the predatros in the last PCOM. The authors concluded that PPR ratio was incostant through PCOMs and that it was influenced both by dispersal events and evolutionary trends in body size. Indeed, the higest predatory pressure values are recorded in conjunction with the increase of carnivore diversity determined by massive immigration episode: the “wolf event” (Azzaroli, 1983; Koenigswald and Werdelin, 1992; Rook and Torre, 1996) occurred at the onset of the Late Villafranchian and some seven new carnivore species appeared at Upper Valdarno PCOM. Then there was the decrease in PPR values that the authors ascribed to the increase of both megaherbivores and small mammals. Indeed, during the Middle to Late Pleistocene,

odd-toed ungulates grew toward the huge size of *Stephanorhinus kirchbergensis*, *S. hemitoechus*, *S. hundsheimensis* and the woolly rhino, *Coelodonta antiquitatis*. These mammals were more than 2 tons in body weight and then, probably, the adults were able to avoid predation. Galerian predators of Europe instead, were not much larger than modern ones, perhaps with the exception of the cave hyena, *Crocuta crocuta spelaea* (Klein, 1986; Klein and Scott, 1989), and the cave bear, *Ursus spelaeus* (Christiansen, 1999) which was exclusively herbivorous (Bocherens et al., 1994; Stiner et al., 1998). Probably megaherbivores monopolyzed a large proportion of ecosystem resource, then reducing the fitness of middle sized herbivores and their abundance. The reduction of these preys lead probably to the decrease in predators abundance. Then the Galerian-Aurelian low PPRs could be determined by both increase of free predator megaherbivores and by the decrease in carnivores's abundance. Moreover, the presence of a small number of middle sized preys determined the opportunity for the increase of small herbivores diversisty. Indee, in these periods there were the first occurrences of species such as the roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), ibex (*Capra ibex*), wild sheep (*Ovis ammon*), and chamois (*Rupicapra rupicapra*). These newcomers seemingly were residing in the smallest size class once occupied by species such as *Gazella borbonica* and *Croizetoceros ramosus* that became underrepresented during Late Villafranchian.

1.2 Materials and Methods

1.2.1 The data employed

The first step towards the aims described in this chapter was the setting of a database with the faunal lists of fossiliferous horizons. The Local Faunal Assemblages were collected using the information provided by 350 specific papers dealing with Plio-Pleistocene mammal faunas and by web databases (http://paleodb.org, for localities in the West and centre Europe; http://www.pangaea.de, for localities in the centre Europe; http://www.helsinki.fi/science/now, for localities in the East Europe). Then, a report was

created for each locality, including the stratigraphic level, the geographical coordinates (all converted in decimal degrees), (where available) the maximum and the minimum age estimation or the radiometric/paleomagnetic age estimates, the youngest available reference and the faunal list. Three kinds of restrictions were considered to select useful localities: temporal, geographical and compositional. The localities collected span in time since the Middle Pliocene to the Early Holocene. As regards the geographical restriction, the LFAs used for the database are located in the Western Eurasia but have a longitude not greater of 60 decimal degrees Est. This restriction is based on two reasons. First, East and most of Central Asia LFAs were excluded because of inconsistent taxonomy (e.g. Chinese LFAs) and, second, Central Asia countries such as Iran, Afghanistan, Azerbaijan are undersampled, although they provided a lot of LFAs belonging to the Neogene. Then, only LFAs with a faunal lists including at least 4 reasonably well identified species were considered (no “cf.” or “sp.” taxa are considered) as, according to Raia et al. (2005, 2006) the statistical analyses performed to detect the paleocommunities are not able to place consistently in the clusters samples having less than 4 items. Finally, only horizons with mammal species belonging to large carnivores (Ursidae, Canidae, Hyaenidae and Felidae), ungulates and proboscideans with an estimated body weight of 7 Kg. at least were collected in the database. Thereby, smaller species belonging to rodents, lagomorphs, mustelids, viverrids, primates, bats, soricomorphs, erinaceomorphs and marine ones were escluded. This restriction was made because the aim of this doctoral thesis is to detect assemblages of mammal species that were subjected to the same degree of taphonomic bias and with strong ecological (read “trophic”) relationships. Indeed, according to Damuth (1982), as for their dimensions, most part of smaller species fossilize with very difficulty. Moreover the choice of species with a strict trophic link is a guarantee to detect assemblages of mammals that really interacted each other, thereby providing the possibility to detect these ecological interactions.

All the procedures described above allowed to collect 811 fossil horizons. Then, another operation was made to avoid the redundancy of same data, such as for taxa found in different horizons of the same locality. Thereby two different horizons of the same stratigraphic section have faunal list that are just one the subset of another, then only the most inclusive horizon was considered. This refinement of the data reduced the available localities to a number of 781. Furthermore another issue concerned the

considered taxa: in many cases in the reference papers, the same species was recorded with different synonyms when found in different localities. This problem was solved by consulting many different specific papers dealing with taxonomy and creating a new database (Appendix A that is provided with a special section with the references used for synonyms) reporting, for each species, all the recorded synonyms and the relative most used scientific name (see Table 1.2 for an examples dealing with *Equus ferus*). Then, an automatic operation updated al the Faunal Lists with the correct scientific names. Finally, the whole database included 781 localities and 220 species of large mammals. All the collected data were used to build a presence/absence matrix, where the information about the occurrences of the selected species in the collected localities were converted in binary code. This conversion was useful for both easily consult the database and to manage the data in the following statistical analyses. Now, it is important to make some remarks about the data used for this research. Dealing with fossil data makes inevitable to consider a possible discontinuity in both temporal and geographical distribution of the fossil record. As regards the time interval, the collected database shows that the most localities are restricted to the late Pleistocene. This is a quite obvious fact because of the higher likelihood to fossilize for younger assemblages and for the well documented collection belonging to archaeological sites and dated to the MIS 3 stage. It is important to say that the temporal discontinuity in the distribution of localities doesn't affect the significance of the computed results. Indeed, the statistical procedure (BCA) used to detect the paleocummunities makes use of an algorithm (UPGMA, see the relative following section) that is able to provide accurate results irrespective of the temporal distribution of the samples.

As regards the issue of the geographical distribution of the LFAs, a statistical method (χ-square) was used to test if this distribution is different from a random one. As a-posteriori observation of the geographical distribution of the paleocommunities showed that these are mainly separated longitudinally, the performed test only considered West-East axis in the distribution of the LFAs. The first step was to compute the geographical coordinates of the centroid of the whole distribution of the localities. Then, the time scale was divided in 500 Ka time intervals, of which reporting the number of LFAs located at the west and at the east of the centroid. At this point statistical operations were employed to compute a possible random distribution of the localities in the west and in the east side of the considered geographical division. The computed simulated

distribution were used as reference data analyze the collected data. A χ-square analysis was used to test if there is a significant statistical difference between the observed geographical distribution of the fossiliferus localities and the simulated random one.

The whole database including all the localities and taxa used in this doctoral thesis is available as supplementary material in Raia et al. (2009).

Valid Taxon	Synonyms
Equus ferus	*Equus antunesi*
	Equus caballus
	Equus caballus mosbachensis
	Equus caballus przewalskii
	Equus caballus przewalskii
	Equus chosaricus
	Equus germanicus
	Equus gmelini
	Equus insulidens
	Equus latipes
	Equus lenensis
	Equus mosbachensis
	Equus przewalskii
	Equus spelaeus
	Equus steinheimensis
	Equus transilvanicus
	Equus uralensis

Table 1.2 Example of the synonyms recorded for *Equus ferus*

1.2.2 Time ordering techniques

1.2.2.1 Spectral ordering

Of the 781 localities useful for the statistical analyses 411 of them reported age estimation data as described above. Then, two kinds of statistical techniques were used to provide time-ordering indexes for all the localities considered that were independent by the ages reported in literature. Next, these indexes were validate by a correlation test with all the available age estimations recorded for the localities. The cited methods were the Spectral Ordering (Atkins et al., 1999) and the Maximum Likelihood

Appearance Event Ordination (MLAEO) (Alroy, 2000). Fortelius et al. (2006) applied, for the first time, the Spectral Ordering technique to fossil data. By using this methodology they provided a new time ordering seriation for the Neogene European localities and, then, they showed that the indexes computed for all localities well correlated with the available ages estimated by radiometric and paleomagnetic techniques.

In the Spectral Ordering the localities recorded in the occurrences database are ordered according to the similarity of their faunal lists. Using mathematical procedures, they ordered along a vector called Fiedler Eigenvector (Fiedler, 1975). Then, a similarity index is assigned to each locality according to their coordinates on the vector. Localities with very similar faunal list have very close position on the vector, thereby they have very similar indexes, whereas localities with different faunal lists are located at the opposite sides of the vector showing, thereby, very different time ordering indexes. These indexes are just numbers and they can assume positive or negative values. Then I will provide a technical dissertation on the meanings and computation of the Fiedler Eigenvector.

Spectral ordering is the operation of ordering data according to a similarity criterion. When applying spectral ordering one faces with the classical “Consecutive Ones Problem” (C1P) (Booth and Lueker, 1976). In a (0, 1) matrix called C, the C1P is the permutation of the matrix C to obtain a new matrix, called IIC, where for each column all the ones are consecutive.

The Fiedler Eigenvector (Fiedler, 1975) was proposed as the solution to C1P in Chung (1997) and in Atkins et al. (1999). In matrix algebra Fiedler Eigenvector, denoted as $v_{n-1} = (v_1,\ldots,v_n)$, is the vector with the second smallest eigenvalue of the Laplacian matrix. The eigenvector v_{n-1} has the property of minimizing the value:

$$\sum_i s(i,j)(v_i - v_j)^2 \qquad 1.1$$

So it minimizes the difference between coordinates of two similar samples (the localities in this case).

For ordering the localities the first step was the calculation of a locality-locality similarity index, computed by the formula:

$$s(x_i, x_j) = \frac{c(x_i, x_j)}{|t(x_i)|^{1/2}|t(x_j)|} \qquad 1.2$$

Where i and j denote the locality; xi is the faunal list of i locality and xj is the ones of j locality; |t(xi)| is the number of taxa in i locality and |t(xj)| the number of taxa in j locality; c(xi,xj) is the number of taxa that occur in both i and j.
Using these indexes the locality-locality similarity matrix S was built. This is a *nxn* symmetric matrix. Then, the diagonal matrix D of S was computed using the software Matlab and the Laplacian Matrix was given by the formula:

$$L = D - S \qquad 1.3$$

Hence the eigenvectors of the Laplacian matrix were easily calculated in Matlab. The following step was the ordination of these vectors from the largest eigenvalue λ to the smallest. As $\lambda_n = 0$, which implies $v_n = 0$, then the λ_{n-1} is the value of the Fiedler Eigenvector. Finally, a spectral index was assigned to each locality according to its coordinate on the vector.

1.2.2.2 The Maximum Likelihood Appearance Event Ordination (MLAEO)

The MLAEO is an algorithm developed by John Alroy (Alroy, 2000) and constitutes the improvement of a preceding one called Appearance Event Ordination (Alroy 1992, 1994, 1996, 1998a,c,d; Wing et al., 1995). It provides the ordination of the fossiliferous localities according the First Appearance (FA) and Last Appearance (LA) of all the species included in the considered faunal lists. This algorithm is similar to the previous one as it includes a procedure to calibrate the localities ordination by using the information provided by geochronological age estimates (although in the new algorithm the procedure is more accurate, see below). The novelty that Alroy provided in MLAEO is that the seriation is evaluated by a maximum likelihood estimate, i.e. the initial candidate appearance event sequence is optimized by procedures reducing nuisance parameters for each given event in the sequence itself.

The MLAEO algorithm is based on the concept of the First Appearance and Last Appearance statement (F/L), that is the pairwise information of the FA of a taxa and the LA of another taxa in the same faunal list. Starting from a (1,0) matrix containing the occurrences of the taxa considered in the localities recorded, the algorithm scrutinises all the FA and LA of the taxa recorded. When two different taxa are included in the same faunal list, they are defined "conjunct" and an automatic procedure records all the information about the FA and LA of these taxa. The algorithm doesn't consider singleton taxa (i.e. taxa that occurred in only one faunal list). Using al the statements about "conjunct" and "not conjunct" taxa the algorithm computes a square pairwise matrix containing all the information about the F/L. At this point, a candidate linear sequence of F/L statements is computed by:

1) using a variant of reciprocal averaging to derive scores for taxa from the F/L matrix
2) using these scores to compute mean scores for faunal lists
3) ordering the lists by their scores
4) computing first and last appearances by scanning across the sequence of lists

Then, a Maximum Likelihood methodology is used swapping each event (i.e. taxa occurrences) are between localities to reduce the "nuisance" parameter for each event in the initial candidate sequence of localities. The final step is to calibrate the computed sequence by the geochronologic age estimates. This procedure creates a model by which fitting the appearance event ordination to the available age estimates for the localities. This model creates an interpolation between these data by using the localities provided of age estimates as "hinges" to "stretch" the ordination and, then, calibrate it. The first version of this model (Alroy, 1996, 1998d) had the weakness of discarding al lot of hinges, then assuming misleading hypothesis of a constant faunal turnover. In 2000, Alroy presented a review of this method called the "shrink-warp" algorithm that allows to use all the available aged localities as hinges to better fit the data to the model. As using many hinges can imply the non-monotonicity of the fitting curve (i.e. a function with consistently increasing and never decreasing or consistently decreasing and never increasing values), the author developed a procedure that creates two fitting curves, one for the decreasing and another for the increasing values. The fitting model, then was built over the mean values between the two curves , this avoiding the non-monotonicity.

1.2.3 The Bootstrapped Cluster Analysis

The Bootstrapped Cluster Analysis (BCA) is a statistical tool useful to detect natural groupings of items and to compute the degree of sharpness for each identified group. This was developed by Pillar (1999) and was already used to detect Italian Quaternary paleocommunities (PCOMS, Raia et al., 2005; 2006a). The BCA is composed by two statistical methods: the Cluster Analysis, that let the detection of the natural groups, and the Bootstrap Resamplig (Efron, 1979, Efron and Tibshirani, 1993), that provides a likelihood for each group identified. Pillar (1999) combined these two techniques to allow the researchers to use the sharpest groups for their analyses. The BCA was used in this doctoral thesis for the detection of the Eurasian paleocommunities spanning in time since the Middle Pliocene to the Early Holocene. At first, I will show how Cluster Analysis works and how it was implemented by Pillar, describing the procedures of Bootstrapped Cluster Analysis and, then, I will discuss how the BCA was used for the aims proposed in this doctoral thesis.

The Cluster Analysis (CA) is a multivariate statistical method that is usually used in many field (naturalistic, medical, anthropologic or social) to gather units, belonging to a determined set, in homogeneous groups, according to the variables characterizing all the considered items. In this analysis each group is defined “cluster”. The method is based on the computation of the distances measured between all the possible couples of items in the contest of the iper-space defined by *q* axes, that represent all the variables of the items. There are different way to compute these distances, according to the kind of analyses to be performed. The most used index is the Mahalanobis distance, that has the important property to take into account the interdependences between all the selected variables. After these distances were performed, then, a distance matrix is built. In this matrix all the diagonal terms are equal to 0, whereas the off-diagonal represents the computed distances. This is the similarity matrix (S) and is defined symmetric as all the values at the correspondent positions in the opposite side with respect of the diagonals are equal. Thus, it is possible to consider, for the analyses, only one of the triangles in which the matrix is split by the its diagonal. There are al lot of algorithms for the Cluster Analysis, but these are generally divided in two kinds of techniques: the “hierarchical” and “non-hierarchical” methods. Only the hierarchical method will be discussed here as it is the one performed for the proposed aims. This methods perform subsequent fusions or divisions of data. The “scissor” method (the one

used here) performs thinner and thinner partitions of the whole sample, finally identifying *n* clusters (Figure 1.4)

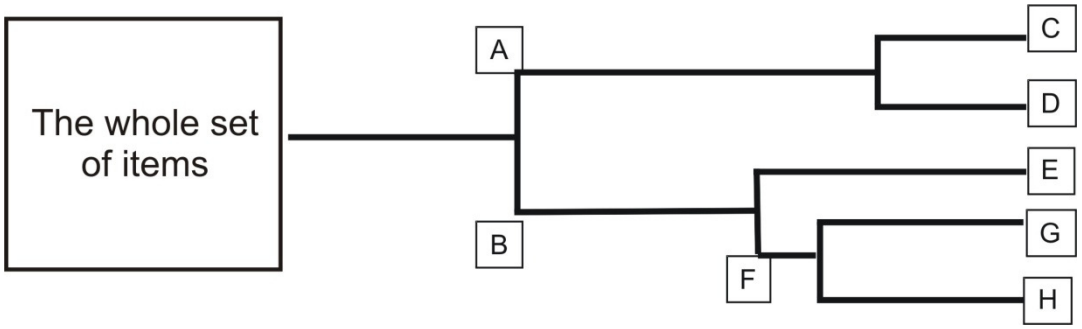


Figure1.4 Schematic representation of the hyerarchical algorithm of the BCA

The Cluster Analysis as described above have two important caveats: the operator has to decide a priori the adequate group partition level; cluster analysis always detects groups, even if the data set does not have a clear group structure (Pillar, 1999). Other methods were developed to solve this questions but, even if some algotithms were able to determine the correct groups in most of cases, their performance was data dependent and there was no evaluation of the criterion "resolving power" (Pillar, 1999). In 1996, Pillar offered the first method to evaluate the homogeneity of the groups in plant community classification by using a probabilistic resemblance, computed by set of randomization under the null hypothesis of random community composition. Later a new general model (the Bootstrapped Cluster Analysis) was provided by the same author (Pillar, 1999). The BCA is based on a set of procedure, called Bootstrap Resampling (Efron, 1979; Efron and Tibshirani, 1993), and performed on the results of a preceding Cluster Analysis. The Bootstrap Resampling is based on the assumption that, in the absence of better information, the distribution of observations in a sample is the best indicator of the distribution in the sampling universe. Than if this assumption is considered true, resampling a sample with replacement will mimic resampling the sampling universe (Pillar, 1999).

In this procedure the operator has to set a range of possible detectable clusters and the algorithm provides the probability needed to evaluate the stability of the partition. After identified as K the maximum number of detectable groups, an iterative algorithm uses the complete samples (the whole presence/absence matrix here provided) and its k-

group partition as reference data. These data are used to compare the other k-groups computed by a successive random resampling of the raw data. In each iteration a new sample of n units is chosen at random (bottstrapped) and then used for a new Cluster Analysis. Than a similarity index called G^* is computed between the reference partitioning level and the new groups detected by the second CA. The second step is to compute a new index G^o based on the null hypothesis that the partition is sharp. The iteration is considered finished with the comparison between G^* and G^o. This single iteration is repeated n times and the greater is n the greater is efficiency of the algorithm. The G^* index is a measure of the similarity between a particular partitioning level and the relative k-partition in the bootstrapped sample. It can assume values between 0 to 1 (when the reference and the bootstrapped k-partitions coincide). The likelihood to recover the reference partition within the bootstrapped sample increase with the likelihood of the reference k-partitions itself to be very sharp. Even if the G^* is near to 1 it doesn't mean that the particular partitioning level is stable. The level of stability of the k-groups is defined by the comparison between the G^* and the G^o index. This latter, as stated above, is computed under the null hypothesis that the groups are sharp, that is to say that the bootstrapped groups are random sample of the reference groups. Starting from this assumption, for each group j with n_j items of the bootstrapped samples, the algorithm samples at random a new group I (called the null bootstrapped sample), with the same number of items of j, from a group in the reference sample that is the nearest neighbor to j. Then, the units of reference sample and the null bootstrapped sample are put together and used to compute a new distance matrix and, thereby the G^o index between these two groups. After a large number of iterations it is possible to define the probability: $P(G^o \leq G^*)$. If $P(G^o \leq G^*)$ is larger than the 5% then it is possible to state that the considered partitioning level is sharp.

1.2.3.1 The BCA applied to the Plio-Holocene Western Eurasia LFAs

Both the occurrences matrix and Fielder Scores were used as entry data for the analyses. The BCA was performed using the Multiv 2.1.2 software (Pillar, 2001). As for the discontinuity of the data used, it was predictable that the number of the localities are not uniformly distributed over the time interval considered in this study. Then, a particular algorithm was used for performing the Cluster Analysis. This is the

Unweighted Pair-Group Method, Arithmetic Averaging (UPGMA) that is able to detect natural groups irrespective of the number of items per group and that detect the separation between the clusters by computing the arithmetical mean distance between them. At first, the BCA was computed at the level of genera and not of species by reducing the 781 localities x 220 species matrix to a 781 localities x 105 genera one. This reduction was justified as recent papers, dealing with the same issue, showed that the BCA recognizes, at the first steps, very large groups that are mainly based on genera-level taxonomic turnover (Raia et al., 2005; 2006a). At the genera-level the Fiedler scores were not included in the analyses as they were computed on the species-level data. In this case the similarity index used was the Jakkard, as it was developed just to operate with binary data.

Once obtained the results of this first analysis, a new BCA was performed on the computed groups, this time operating at the species level and including the Fielder scores too. In this case the Gower Index was used as distance metric as it was developed to operate with multiple kinds of variables (nominal, continuous or binary entry data). The level of significance to evaluate the sharpness of the clusters was fixed to 0.05. In interpreting the results the status of Eurasian Paleocommunity (EA PCOM) was assigned to level of partitioning with the probability value just greater than the significance level. The motivation of this restriction is justified by the interest of this project in obtaining the finer level of partitioning.

1.3 Results

1.3.1 The time-ordering of the Local Faunal Assemblages

The correlation between Fiedler scores and geochronologic ages (Figure 1.5a) provids a very high Pearson Product Moment (R^2=0.968; p = =1.591*10^{-294}) with a significant relative regression (F = 11,930; b = 11,636,613.222; n = 392). The correlation between ML AEO scores and geochronologic ages (Figure 1.5b) provides similar results with R^2 = 0.918; p = 1.735*10^{-214} and the relative regression shows the following statistics: F= 4360.04; b = 12,992.599; n = 394. The correlation between Fiedler scores and ML AEO scores (Figure 1.5c) is very high and statistically significant (R^2 = 0.915; p =

$1.632*10^{-203}$) showing that the two methods are quite similar in the results they provide. For the BCA only the scores computed by Fiedler Eigenvector were used as entry data along with the presence/absence matrix, because they provided the higher correlation coefficient and for the mathematical procedures to compute them work with the same identity matrix (D, described above) used by the BCA for the detection of the paleocommunities.

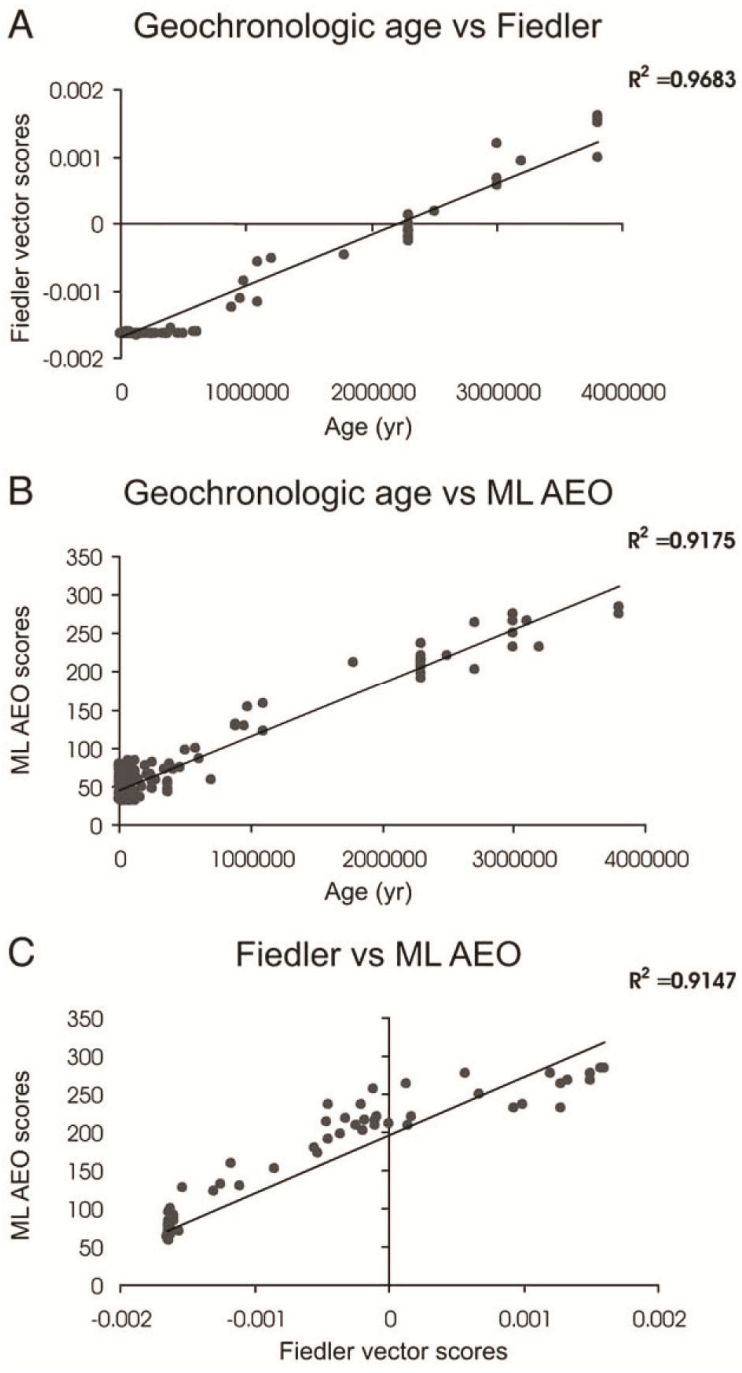


Figure 1.5

1.3.2 The EA PCOM

When interpreting the results of the Bootstrapped Cluster Analysis, only the detected groups with a probability value just greater of the significance level were considered.The first BCA employed at the genera level provided two great groups: G1 and G2. The subsequent BCA performed on these groups divided the former group in two clusters: G1.1 and G1.2. The latter was further divided in G1.2.1 and G1.2.2. The G2 was divided in two parts: C2.1 and G2.2. The former did not undergo other divisions while G2.2 was divided in two sub-groups: G2.2.1 and G2.2.2. The BCA performed on the former provided other 3 sub-groups: G2.2.1.1; G2.2.1.2; G2.2.1.3. The Figure 1.6 shows a graphical representation of these subdivision (the length of each branch have only a graphical meaning), whereas the Figure 1.7 shows the trends of the statistical significance of the clusters during the bootstrap resample. The bold lines represent the stable groups.

Each of the statistical stable cluster was defined EA PCOM. A total of 8 EA PCOMs were detected. Starting from the older, the EA PCOM 1 is represented by the cluster G2.1, spans in time since 3.7 to 3.0 May and correspond to the “Early Villafranchian”. The following EA PCOM 2 is represented by the cluster G2.2.1.1, ageing since 2.5 to1.9 Mya and including LFAs dated to the first part of the “Middle Villafranchian” while the EA PCOM 3 (G2.2.1.2) corresponds to the second part of the “Middle Villafranchian” (2.2 to 1.5 Mya). The EA PCOM number 4 is identified by the cluster G2.2.1.3 and covers the time interval since 1.9 to 1.3 Mya. This is can be ascribed to the time period covering “early Late Villafranchian” to “middle Late Villfranchian. The following EA PCOM 5 (G2.2.2; age span: 1.8–1 My) covers “middle Late Villafranchian” to “late Late Villafranchian”. It includes localities such as Ceyssaguet, Colle Curti, Venta Micena, Pirro Nord, and Sainzelles. EA PCOM 6 (G1.2.1) includes “late Late Villafranchian” to “Early Galerian” localities (1–0.3 Mya). The EA PCOM 7 spans in time over most of “Galerian” (0.6–0.068 Mya). EA PCOM 8 Compraises includes the most localities and spans in time since the latest Galerian to Early Holocene. In the Table 1.3 there is a summary report of the 8 EA PCOMs showing some of the most important localities they include.

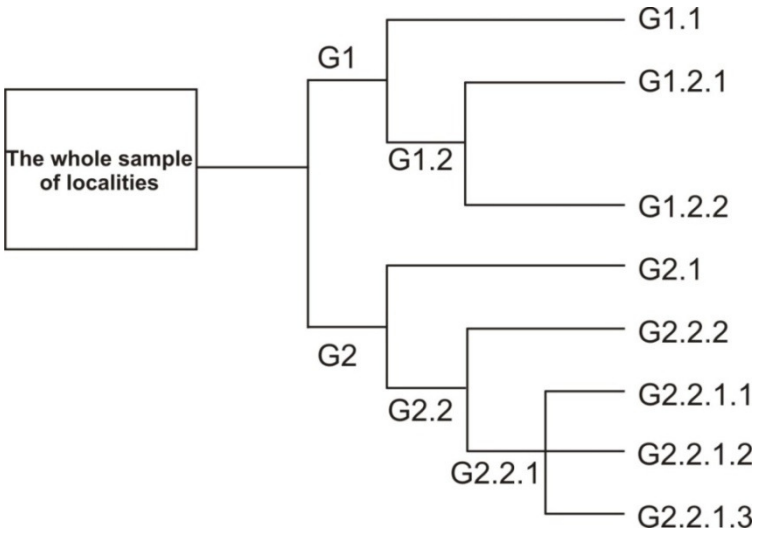


Figure 1.6 Graphical representation of the subsequent and hyerarchical partitioning of the clusters

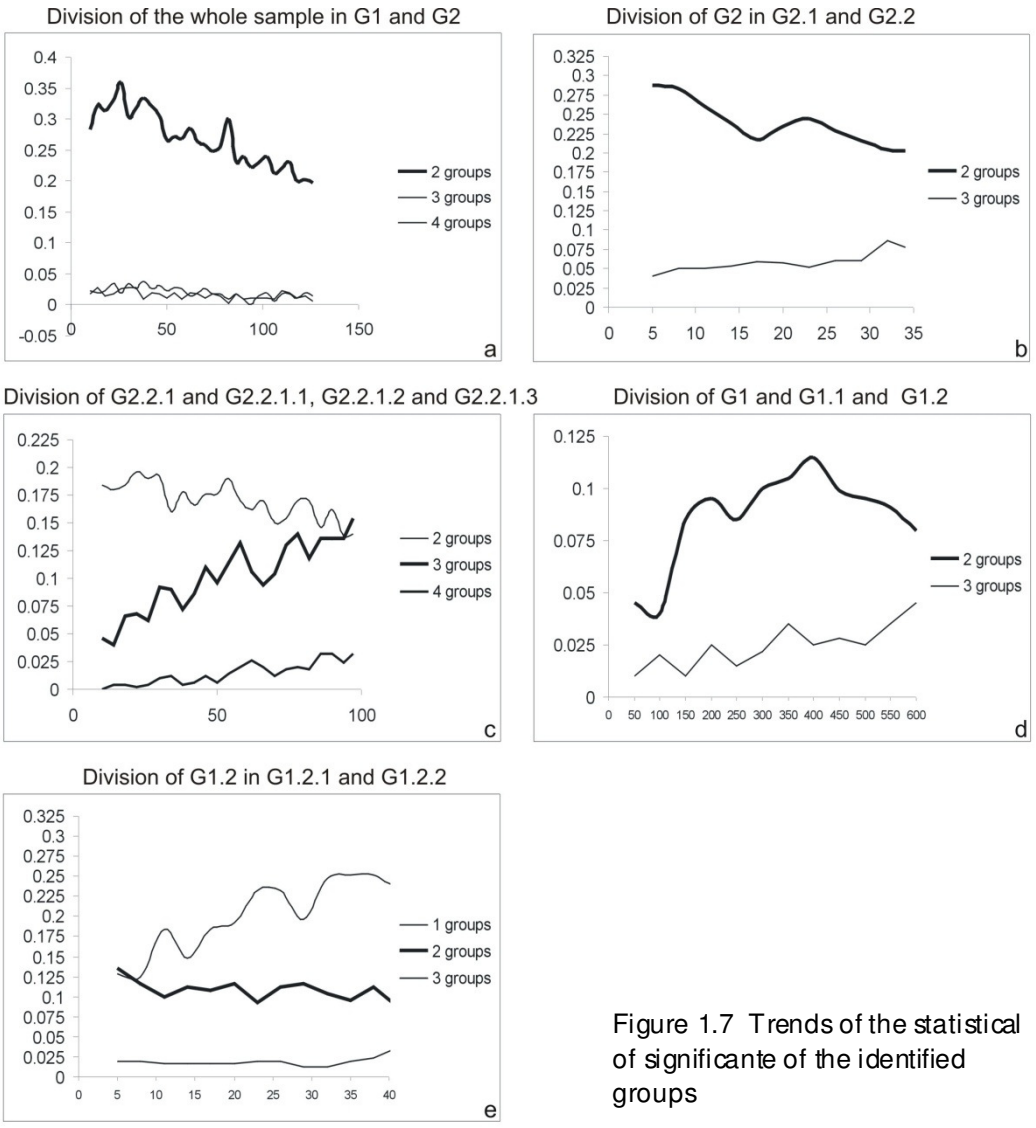


Figure 1.7 Trends of the statistical of significante of the identified groups

EA PCOM	Cluster	Time span (Mya)	Most important localities
1	G2.1	3.7 - 3.0	Triversa, Capeni, Tulucesti, Les Etouaires
2	G2.2.1.1	2.5 - 1.9	Saint Vidal, Coupet, Norwich Crag
3	G2.2.1.2	2.2 - 1.5	Saint Vallier, Montopoli, Dmanisi, Tegelen
4	G2.2.1.3	1.9 - 1.3	Psekups, Fonelas P1, Poggio Rosso Pantalla
5	G2.2.2	1.8 - 1.0	Ceyssaguet, Colle Curti, Venta Micena, Pirro Nord, Sainzelles
6	G1.2.1	1.0 - 0.3	Voigstedt, Suessenborn, Tiraspol, Pakefield Rootlet bed
7	G1.2.2	0.6 - 0.068	Orgnac 3, Lunel Viel, Isernia, Mauer
8	G1.1	0.4 - 0.006	Adler cave, Ambrona, Atapuerca, La Ferrassie, Heppenloch, Abri de la Madeleine, Roc de la Melca

Table 1.3 EA PCOMs, their time interval and localities

1.3.3 The geographical distribution and composition of the EA PCOMs

The results provided by the χ-square test (Table 1.4) show that almost all the identified EA PCOMs have a geographical distribution of LFAs that is not influenced by taphonomic bias. Only the time interval marked by an asterisk seems to have a distribution statistically different from a random expectation. In particular, the whole time interval covered by EA PCOM 1 shows to have a number of localities in the west side that is smaller than expected. The same kind of problem affects the time period spanning since 1.5 to 1 Mya. This temporal interval includes part of the EA PCOM 4 and the whole EA PCOM 5.

EA PCOM	Time interval	E	W	Expected E	Expected W	Total
6, 7, and 8	0–500 ky	128	441	128.2	408.8	537
6 and 7	500 ky–1 My	2	12	1.9	6.1	8
4 and 5	1–1.5 My	3	24	3.1	9.9*	13
2, 3, 4 and 5	1.5–2 My	12	24	11.9	38.1	50
2 and 3	2–2.5 My	2	8	1.9	6.1	8
1	3–3.5 My	11	4	11.0	35.0*	46
1	3.5–4 My	3	1	3.1	9.9*	13
Totals		161	514	161.0979	513.9021	675

Table 1.4 Results of the χ-square test. Asterisks indicate the significative differences

The EA PCOM 1 includes 24 localities and 49 taxa. In Figure 1.8 the localities are shown by their Fiedler score. The red-coloured localities are the youngest, whereas the orange one are the oldest. According to their Fiedler scores (the relative-estimated age) It is possible to observe that there is no spatial pattern in the distribution localities. In this EA PCOM the most abundant species are *Anancus arvernensis*, *Mammut borsoni*, *Tapirus arvernensis*, *Stephanorhinus jeanvireti* and *Rusa rhenana.* The EA PCOM 2 (Figure 1.9) includes 12 localities and 27 taxa. The localities are located everywhere in its geographical range and no spatial pattern is detected in their scores distribution. The most common taxa are *Mammuthus meridionalis* and the rhino *S. etruscus,* whereas *A. arvernensis* also persists. A biochronological observation is that the onset of paleocommunity coincides with the "*Elephant-Equus* event" (Azzaroli, 1988; Koenigswald and Werdelin, 1992).

As regards the EA PCOM 3 (Figure 1.10), it includes 49 taxa. The 23 localities are mainly found in the western and southern part of Europe. The distribution of Fielder scores doesn't empahsize any spatial pattern. The most abundant taxa are *Eucladoceros ctenoides*, *Equus stenonis*, *Pliocrocuta perrieri*, *S. etruscus* and *M. meridionalis.*

The previous and the following EA PCOM 4 (Figure 1.11) overlap in time for some 400 Kya, the latter including 27 localities and 45 taxa. Its assemblages differs from the EA PCOM 3 by the presence of *C. etruscus*, the fallow deer *Axis nestii* and the bovid *Leptobos etruscus,* but includes some taxa already present in previous paleocommunity (*E. stenonis*, *S. etruscus*, *M. meridionalis Pachycrocuta brevirostris*). The geographical

range of EA PCOM 5 (Figure 1.12) spans mainly in the South and Western Europe and includes 17 LFAs and 44 taxa. This paleocommunity plainly marks the lates Villafranchian. The spatial pattern of the EA PCOMs 4 and 5 were not discussed because, as showed by the χ-square test, the distribution of the localities could be influenced by sampling or taphonomic biases. The two following EA PCOMs are very interesting. The EA PCOM 6 (Fig. 1.13) includes 23 localities and 43 taxa. The LFAs are located in the in the North-Eastern part of Europe. The most common species are *M. trogontherii*, *S. etruscus*, *Praemegaceros verticornis*, *Cervalces latifrons* and *Cervus elaphus*, and there is the first occurrence of *Elephas antiquus, Equus ferus, Stephanorhinus kirchbergensis* and *Sus scrofa*. The almost contemporaneous and slightly younger EA PCOM 7 (Figure 1.14) contains 48 taxa and 32 LFAs. These latter are located in the Central and Western part of Europe and the most common taxa are *Cervus elaphus, E. ferus, S. scrofa, E. antiquus, S. kirchbergensis, Dama dama, Equus hydruntinus, Hemitragus spp., Mammuthus primigenius, Panthera leo, Megaloceros giganteus, Rupicapra rupicapra, Ursus spelaeus, S. hemitoechus.* The observation of the geographical distribution of the EA PCOMs 6 and 7 highlights that these paleocommunities are examples of a compositional turnover. The youngest LFAs of the EA PCOM 6 are located in the Eastern and Northern part of its geographical range including tipically Galerian species. It is possible to observe that the same fauna become abundant in the following EA PCOM 7 and here is located in the Western and Southern part of Europe. It probably represents a migration event of mammals coming from the eastern region of Eurasia and that disperse in the Central and Southern part of Europe.

The EA PCOM 8 (Figure 1.15) has the largest number of LFAs. This is not surprisingly and prevedible for the reason discussed above. It includes 537 LFAs and 49 species. The localities are located over the whole geographical range considered for this research project. It is evident that, observing the distribution of the Fiedler-based estimated ages, that the oldest LFAs are mainly located in the Western and Southern part of the considered geographical range, whereas the youngest are located in the Northern and Eastern part. This pattern is interpreted as a post-glacial recolonization by mammals of the northern localities, tipically of the Holocene. It is worth to note that the recorded diversity of this youngest paleocommunity is very similar to the oldest one.

This means that the statistical methods employed provide results plainly comparable, thus allowing any macroecological and evolutionary hypotheses testing between them.

Figure 1.8

Figure 1.9

Figure 1.10

Figure 1.11

Figure 1.12

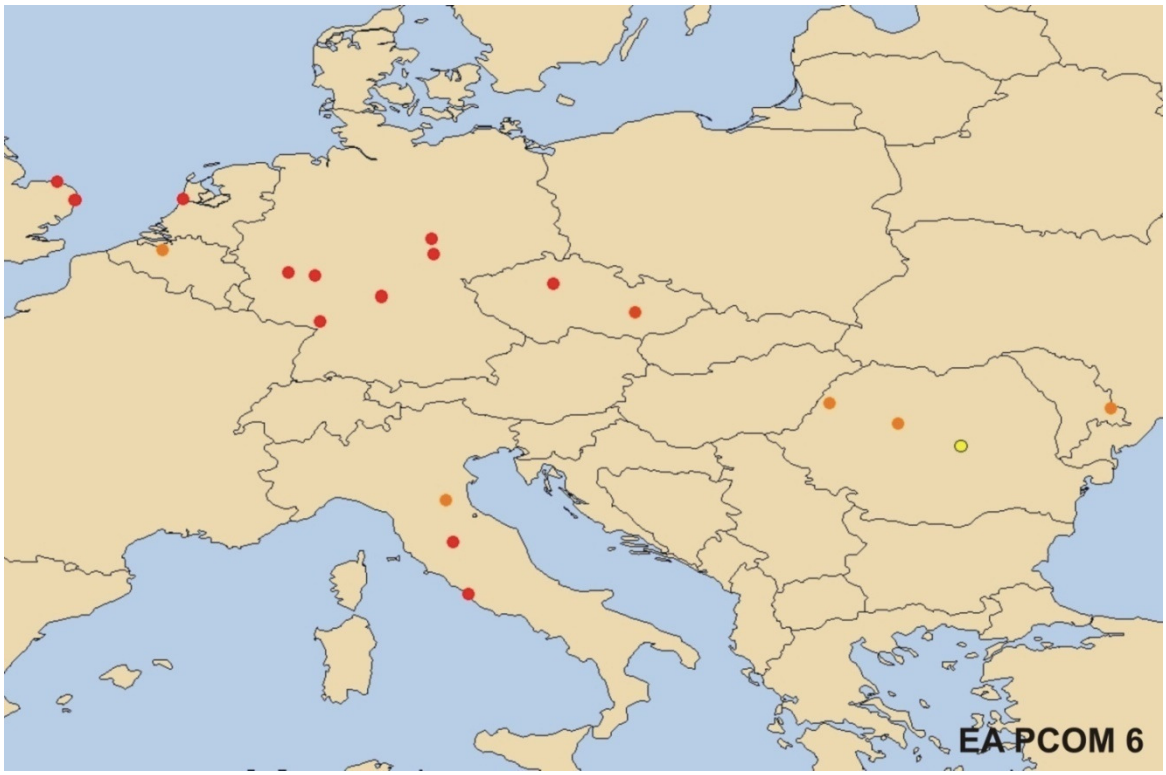


Figure 1.13

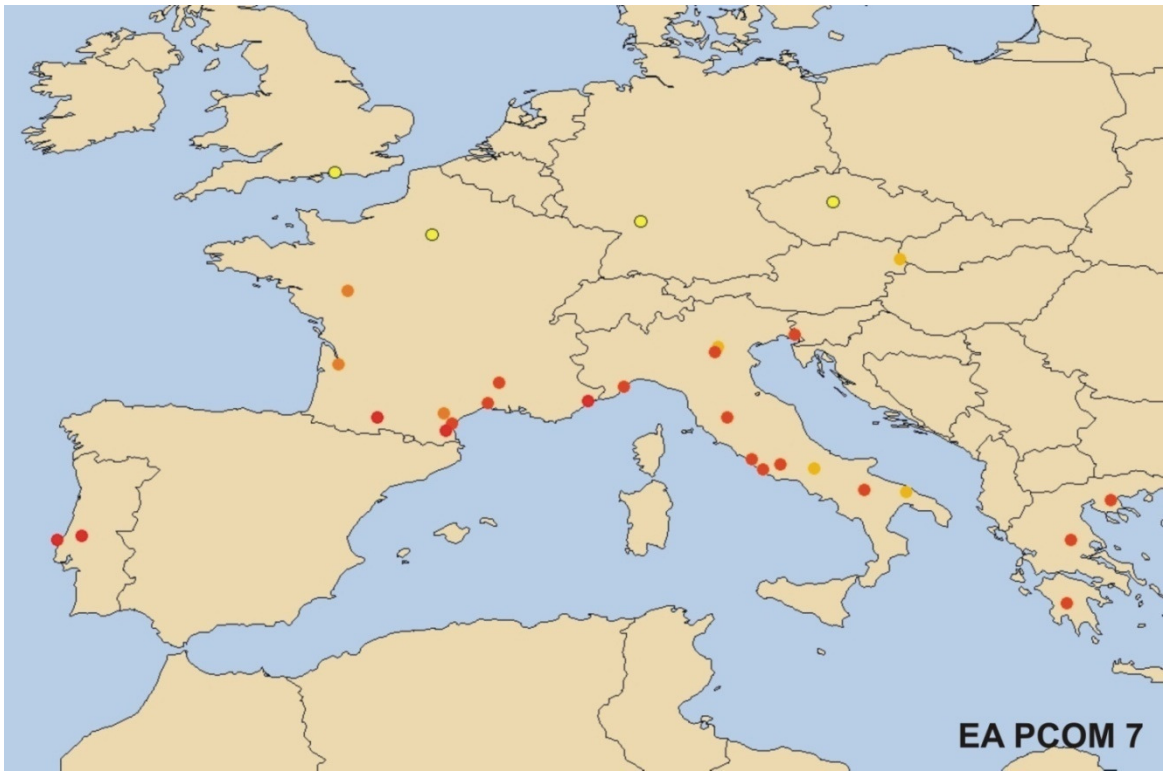


Figure 1.14

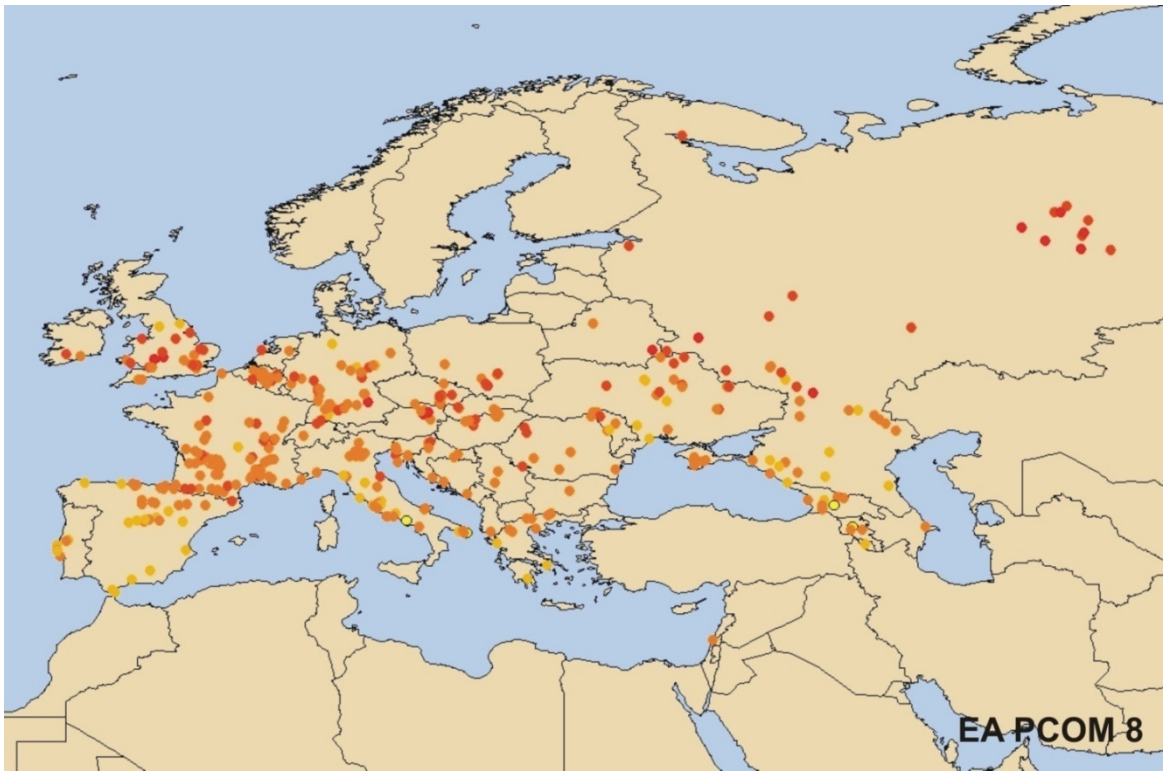


Figure 1.15

1.4. Discussion

This research has dealt with the detection of fossil mammal communities. To this aim only statistical analyses were employed to satisfy the need of having objective schemes that identifies fossil mammal assemblages. As discussed in Lindsay, 2003 and in Raia 2006, biochrons provided for vertebrate palaeontologists are not suited for such kind of studies. The problem of the diachrony related to biochronologic schemes forces palaeontologists to provide reference species to determine temporal boundaries. The EA PCOMs are not biochrons and, thereby, they don't suffer of such limitations. They are provided of both spatial and temporal resolutions, and, by this latter, they are an improvement of the previous detected Italian PCOMs. Indeed, the Italian paleocommunities had a too narrowed geographical breadth to embrace the total distribution of the taxa analyzed. Then, they were not able to embrace the territories covered by mammals during their dispersal events. EA PCOMs seems to enclose a territory enough large to detect spatial turnover. The distribution of the index-based time ordering of the LFAs in the EA PCOM 6, 7 and 8 are clear examples of the possibility they provide "to catch" mammals moving over time and over land to find more suitable habitat. The inclusion of a time ordering score for each localities has given the opportunity to increase the sample size of LFAs, this increasing the power of any statistical tests. It is worth to marks that EA PCOM and Biochrons are different fo the aims they were built. Biochrons are the most suited tool provided to palaeontologists to permit the correlations of stratigraphic units and are irreplaceable in depicting faunal succession in time.

EA PCOMs are drown to serve for macroecological and evolutionary hypotheses testing. Apart the results of Raia et al. (2005, 2006), no such ecological-sound frameworks has been provided yet to vertebrate palaeontologists to study the evolution of the mammal assemblages. The Eurasian Paleocommunities of the Plio-Holocene need to be further investigated. Besides the macroecological investigation, other new filed could put to the test them, such as the new phylogenetic wave to the aim of detecting the phylogenetic structures and differences of the fossil mammal communities.

Chapter 2 -Macroecology of the fossil mammal assemblages: occupancy, range size and phylogeny

2.1 Introduction

Macroecology seeks to develop an understand ecological systems through their study as a whole (Gaston and Blackburn, 2000). This large-scale approach has the advantage that it takes sufficiently distant view of ecological systems that the idiosyncratic details disappear, showing only generalities (Brown, 1995). Macroecologists are interested in detecting patterns in species body size and abundance distributions, and in body size-range size and in occupancy-range size relationships. Even if most of these kind of researches were at first conducted on living organisms, some studies applied macroecological hypotheses testing to fossil data. Indeed, working with fossils allows detecting patterns on a longer time interval than that considered for living taxa. This provides benefits to study evolutionary patterns in past communities and to depict possible trends in the history of organisms. For example, long term studies have shown the peaked trend for both occupancy and range size during the taxon life. As regards the peaked trajectory of the range size, Miller (1997) discussed the possibility that the expansion of range sizes at the genus level could be due to either geographical expansion of the constituent taxa or to the addition of new ranges due to speciation events.

Other studies proved there is a strong correlation between occupancy and duration for both species and genera (Cardillo and Bromham 2001; Cardillo et al., 2003; Jablonski and Hunt, 2006; Powell, 2007; Foote et al., 2008), inferring that abundant taxa are able to overcome stressed conditions determined by strong environmental changes. Range size was also found to be correlated with taxon duration (Foote et al., 2008) but the authors found no evidence to determine if range size influences duration or vice-versa.

In this chapter I will investigate about macroecological patterns of large mammal faunas lived in Western Eurasia since the Late Pliocene to the Early Holocene. All the analyses will be performed used the data collected in the presence/absence matrix of taxa and fossiliferous localities describes in the previous chapter. In particular, the statistical test will be employed as follows:

- To detect the occupancy and range size trajectories of both species and genera considered;
- To draw a general model depicting the most frequent occupancy and range size trajectories of the taxa analyzed;
- To test if phylogenetically closely related taxa have an overall geographical position that is closer than by chance;
- To test for the hereditability of body size, taxon duration, occupancy values, range size values for both species and genera;
- To test the correlation between all the features computed via independent contrasts;
- To test, according to Miller (1997), if the recorded variation of geographic range sizes during the genera duration was due either to the addition of new species to the original pool or to the geographical expansion of the constituent taxa.

A discussion on macroecological issues such as the distribution of the body sizes, occupancy and range sizes follows up, focusing on some mile-stones papers that illustrate the macroecological hypotheses testing in both ecological and paleoecological fields. All these discussed features are widely analyzed in the literature and many studies show that they strongly interrelate providing linkage between local scale and large scale ecological investigations. Also I will give a special attention to the recently born comparative methods (statistical techniques that account for phylogenetic effects in comparisons among biological entities).

2.1.1 The body size and its geographical distribution

The size of an object is one of the principal ways by which we classify and judge it. Ecologists record body sizes as just as a journalist report's people's age (Nee and Lawton, 1996). Most life history traits of animal species are strongly correlated with their body size (Peters, 1983; Calder, 1996; Harvey and Pagel, 1991). Moreover, body size has the significant advantage that is comparatively simple to measure reliably. The distribution of the body sizes of the species in an assemblages is a useful indication of the characteristics of a community (Gaston and Blackburn, 2000). For these reason the body sizes is one of the possible attribute of an organism that is most studied in the

ecological, paleontological and evolutionary literatures. Indeed, being a subject of interests, the frequency distribution of animal body sizes has been reported for many animal taxa.

At small scale of investigation the frequency distribution of the body sizes are normal or right skewed (Brown and Nicoletto, 1991; Blackburn and Gaston, 1994; Brown, 1995; Gaston and Blackburn, 2000).

At large spatial scales the distributions of body sizes are typically log right-skewed. In 1959, Hutchinson and MacArthur plotted the frequency distributions of body sizes among the species of land mammals of Michigan and Europe. They noted that these distributions were highly skewed, such that there were many more species of relatively small mammals than of large or extremely small ones. They suggested that this pattern effected the capacity of the modal-sized species to be relatively more specialized, and hence to subdivide space and resources more finely. Groups of organisms as different as bacteria, trees, insects, fishes, and mammals all show the pattern described by Hutchinson and MacArthur.

According to Maurer et al. (1992), the genera of terrestrial mammals show log right-skewed pattern in assemblages of “very large” continents (Eurasia, Africa, South America, North America), but not significantly skewed for assemblages of “smaller” ones (e.g. Australia, New Guinea, Madagascar), because of the absence of large-bodied genera from the small land masses. According to a personal opinion, these kinds of comparisons, for these latter special cases, need to be further explored.

2.1.2 Occupancy

Occupancy is defined as the proportion of sites where a species is actually found within a given sampling area. Some authors pointed out that occupancy is a scale dependent property of species as at a local geographic scale its frequency distribution is bimodal while at a wider (regional scale) it is unimodal and right skewed (McGeogh and Gaston, 2002). The same authors affirmed that at local scale the occupancy frequency distribution shows this pattern as it follows the Raunkiaer’s law, according to which, at local scale, most species are either very common or very rare, either. Raia et al. (2006) used this local pattern of the occupancy frequency distribution to test if Quaternary large mammal communities follows the Raunkiaer’s law. The pattern showed by occupancy

frequency distribution at a regional scale implies that most species are found in just a few sampled sites.

Some studies (Gaston and Blackburn, 2000; Gaston, 2003) found a very close relationship between local occupancy and range size of avian species. Other studies showed that species range size correlates well with long-term species survival as a species that covers a very large geographical territory has a higher likelihood to found refugia and, thereby, a good chance to overcome extinction risk (Cardillo and Bromham, 2001; Cardillo et al., 2003) This relationship provides a link between occupancy and local species survivor. This is of great interest for conservationists trying to model species extinction risk on actual occupancy data. Other studies demonstrated that occupancy is not constant over species existence. In most cases the occupancies values computed in different time intervals of a species life span draw a peaked trajectory with its maximum occurring halfway along a taxon duration (Raia et al., 2006; Foote at al., 2007; Liow and Stenseth, 2007).

2.1.3 The abundance-occupancy relationship

Local abundance and occupancy are correlated in many taxa (Gaston and Blackburn, 2000; Freckleton et al., 2006). This relationship is a positive one in the most cases as species locally abundant are also found in many sites of the sampling area. This relationship is not sensitive to the size of the organisms considered as it was found in birds (Gaston et al., 1999a, 1999b), in fish (Flebbe, 1994) and in Lepidoptera as well (Cowley et al., 1999). The importance of both abundance and occupancy grew up more and more as they showed a strict relationship with other macroecological patterns (Gaston and Blackburn, 2000). Moreover they provide a linkage between local (abundance) and larger (occupancy) geographical scale (Freckleton et al., 2006) allowing a cross-scale macroecological hypotheses tensting. Some authors stated that differences between abundance-occupancy relationships between species are due to possible differences in large-scale population organization. Indeed, Freackleton et al., (2006) pointed out that metapopulations (i.e spatially separated populations of the same species in a patched environment, that interact each other also by gene flow, Levins, 1969) and non- metapopulations may show differences in this relationship as for their own particular population dynamics.

Exceptions in the abundance-occupancy relationships are also known. For example, British vascular plants do not show any such relationships and this is interpreted to be due to the lack of long distance dispersal ability of these populations.

Many authors provided different explanations for this positive relationship, which they have explained in terms of metapopulation dynamics (Hanski et al., 1993; Hanski, 2000), realized niche breadth (Brown, 1984; Hansky et al., 1993; Gaston et al., 1997) or latitudinal effects (Gaston and Blackburn, 2000), but no one of these hypotheses have provided a convincing explanation.

Three very important studies provides statistical models to describe a possible mechanism for the positive abundance-occupancy relationships. Holt et al. (1997) proposed the first model based on basic demographic processes. Their model is based on the assumption that if one varies the habitat conditions by increasing the finite rate of population growth, this will affect simultaneously the density of individuals within habitat patches and the number of habitable patches (a measure of the occupancy). This statistical model it suffer the limitations of its assumptions. Indeed, Holt et al. (1997) assumed that the quality of the habitat was uniform, meaning that high, intermediate and low quality habitat parches could occur with the same likelihood. But this is not as true as assumed. Thomas and Kunin (1999) showed that habitats and populations are fragmented and that habitat suitability varies spatially, while other studies showed the importance of the colonization and dispersal in the dynamics of populations in patchy landscapes (Venable and Brown, 1993; Kot et al., 1996; Thomas and Kunin, 1999; Bullock et al., 2002).

Freckleton and collaborators (2005) tried to include this sort of large-scale population dynamics in their model founding that either the strength and the shape of the abundance-occupancy relationship strongly depend on the ability of the species to colonize habitats. Indeed, when the colonization rates are high the relationship simply follows a saturation forms, whereas at lower colonization rates, the colonization and extinction of habitat patches have an balancing effects and then the local population is maintained by metapopulation dynamics. Again, in 2006, Freckleton et al., proposed to modify the Holt et al.'s model also including a measure of the habitat suitability to seek at what degree this latter affects the relationship between abundance and occupancy. They created an index of the habitat suitability based on vital rates computed on

population data coming from the British Trust for Ornithology Common Birds Census collected between 1962 and 2001.

They concluded that there is no reason the state that the relationship between abundance and occupancy should be strong in any cases. Indeed they found that the strength of this relationship depends on the distribution of the habitat suitability. In their model a weak relationship is expected to occur when species can occupy patches even at low densities. Moreover they pointed out the importance of the précis value of the slope of the relationship as it is found to be closely related to the shape of the distribution of the habitat suitability.

2.1.3.1 Occupancy in paleontological studies

There are few but very important studies analysing the patterns showed by the occupancy of fossil species. These are of great interest because they provide information on the macroecological patterns of extinct taxa but also show the modification of the occupancy during taxon life time span and during evolutionary time intervals.

In 2006, Raia and his collaborators studies macroecological patterns in Quaternary large mammal faunas of the Italian peninsula. In their paper they set these macroecological analyses on statistically discrete fossil paleocommunities they called PCOMs, computed with the same statistical techniques employed in this doctoral thesis to detect the EAPCOMs. The authors performed many statistical tests to detect the pattern of the Italian mammals occupancy frequency distribution, to test a relationship between taxon occupancy and its relative duration and to draw, for each taxon, the trajectories of occupancies' values computed in each subsequent PCOM. In particular, for this latter aim, they concentrated on the "peaked" trajectories they defined as any graphical course showing the maximum value not coinciding with either the first or the last occupancy values and occurring somewhere in the middle of the trajectory. The results of this study showed that most PCOMs have a unimodal right skewed occupancy frequency distribution, a typical pattern expected for large geographical scales, while some PCOMs (U Valdarno, V di Chiana, Pirro and Galerian 1 PCOMs) showed bimodal distribution (Figure 2.1 from Raia et al., 2006, pag. 188). Moreover they found the peaked occupancy trajectory to be the most frequent (63,1%) for the taxa

analysed. Surprisingly the authors found this predominant pattern to be nearly exclusive of hervibores, while most carnivores showed non-peaked trajectories. Another very interesting results of this work was the high correlation between maximum occupancy values and taxon duration ($r = 0.501$, $p < 0.001$) they reported. Their interpretation of the results proved a macroecological role for Italian PCOMs. They confirmed that PCOMs followed the Raunkiaer's law for those showing a bimodal occupancy frequency distribution. The same authors interpreted the non-bimodal patterns of the post-Galerian PCOMs as the results of the influence of the increasing cold climate started some 1 Mya and that negatively influenced the abundance of the taxa considered (Raia et al., 2006). Moreover, they found a strong correlation between taxon maximum value of occupancy and its duration. They explained this results invoking the Brown's generalist hypothesis (Brown, 1984), according to which species with larger range size (read higher occupancy values) are more "habitat-generalist" and, therefore, have less extinction likelihood risk as they can repair in different sites.

Another study on occupancy trajectories in fossil taxa was provide by Foote and collegues (Foote et al., 2007). In their work they studied the occupancy trajectory of Cenozoic marine fossil molluscs of the New Zeland. The great deal of data allowed them to consider 2023 species and sub-species and 608 genera and sub-genera. The authors computed the occupancy trajectories for the taxa considered and found that the most of them showed a peaked trajectories, according to the results of Raia et al., 2006. In Foote et al. (2007), the provided results showed that, as regards the peaked trajectories, the maximum computed value of the occupancy fell somewhere in the intermediate part of the taxa life span. Moreover, genera reached higher maximum values of occupancy than those computed for species and these differences were ascribed to the fact that genera occupancy is computed over many species, thereby there is no biological meaningful for genera trajectories (Foote, 2007).

Nevertheless, the importance of the biological meanings for species trajectories, together with their symmetrical waxing and waving shape, could provide important insights for predicting species extinction risks.

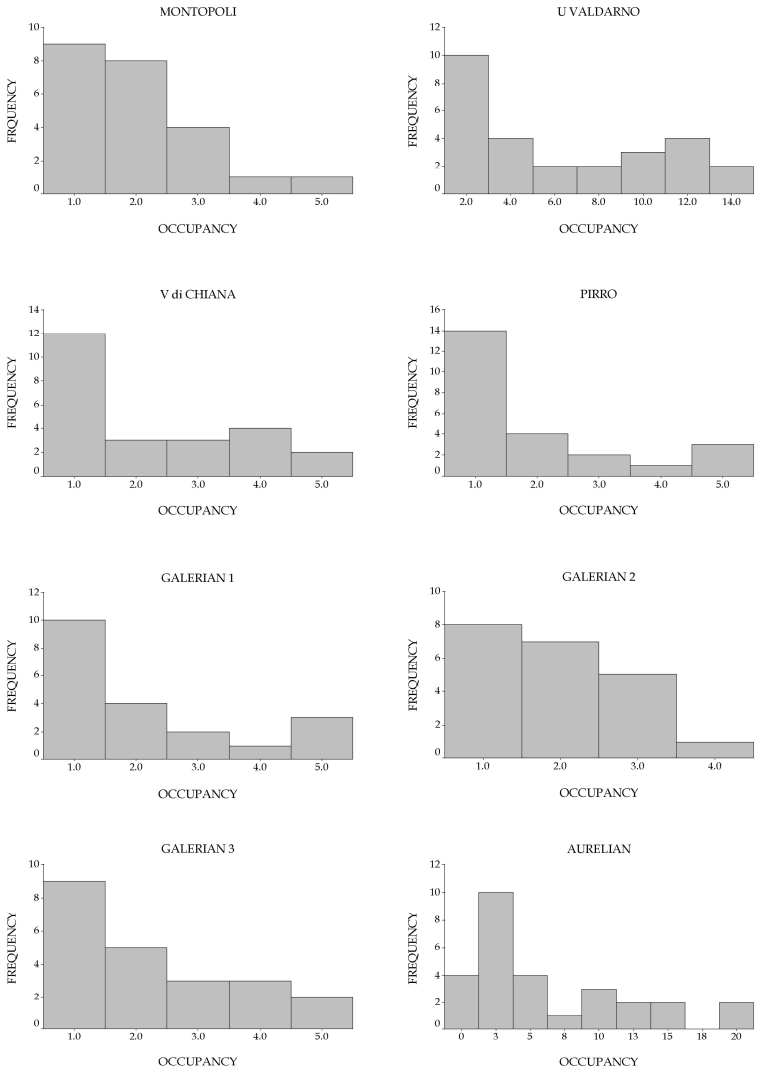


Figure 2.1 The occupancy frequency distribution in italian PCOMs

2.1.4 The range size

The range size is an important property of the taxa as it depends mainly on the dispersal ability and on the niche breadth of the considered species. These latter properties determine the distribution of the species populations at regional scale and influences directly taxon occupancy.

Rapoport in 1982 wrote that: "…geographical areas of distribution are the Chinese-lantern shadows produced by the different taxa on the continent screen: it is like measuring, weighing, and studing the behaviour of ghosts" This statement makes the difficulty of computing range size very evident. At first it is important to define what is the

range size. As pointed out by Gaston (1991d, 1994b), range size has two definitions according to the field of application. Indeed, it is considered as the area between the outmost limits of the occurrence of a species and as the area over which a species is actually found. The former, defined the extent of occurrence, is used in field guide while the latter, based on the area of occupancy, is used for more specialist studies and represents the more accurate measure of range size. Generally, the area of occupancy is smaller than the extent of occurrence as it only consider the areas of the surface were the species occurrence is effectively recorded, thereby it tends not to incorporate in this measure the territories and habitats not coherent with the taxon ecology. The finer is the sampling resolution (depending on the sampling efforts) the larger is the difference between the area of occupancy and the area of occurrence. In studies concerning living species the term range size is used as a synonym of area of occupancy. As for fossil site the sampling efforts mainly depends on taphonomic bias, in paleontological studies the range size measured often closer to the definition of area of occurrence. In this doctoral thesis I will use some corrections for computing the range sizes for fossil species just to make these measures the more possible closer to the area of occupancy (see material and methods in this chapter).

As discussed for occupancy, some studies confirm that the computation of the geographic range sizes in different moment of a taxon life let in most cases to draw a peaked trajectory for this feature (Miller, 1997; Gaston, 1998; Webb and Gaston, 2000; Roy et al., 2001; Ricklefs and Bermingham, 2002; Jones et al., 2005; Liow and Stenseth, 2007). Instead, other studies still report examples of constant range size over most of species' life (Jablonski, 1987; Vrba and deGusta, 2004). Both the occupancy and range size trajectories will investigated in this chapter to the aim to draw a general model of the most frequent pattern in fossil data.

2.1.4.1 The distribution of range sizes

The geographical distribution of range size in extant species has shown two different patterns when considering different geographical scales for sampled areas (Gaston and Blackburn, 2000). At the local scale, the distribution showed a bimodal pattern with both wider and narrow distribute species being the most frequent (Raunkiaer, 1934; Goodall, 1952; Hanski, 1982a-c; Gotelli and Simberloff, 1987; Williams, 1988; Collins and Glenn,

1997; Tokeshi, 1992; Gaston, 1994). For British birds, bimodality tends to be more pronounced when sites are more similar and more species can occur at all sites (Gaston and Blackburn, 2000). At larger geographical scales, the range size distribution shows an unimodal and right skewed pattern with the rare and narrowly distributed species being more frequent than those with larger range size. A log-transformation of these data can convert the right skewed pattern in a symmetric one, but in some case, such as for British birds, a logit transformation could provide the best conversion for obtaining a symmetric pattern. At the regional geographic scales the right skewed distribution is confirmed both for extant assemblages (e.g. for birds Anderson, 1984; Blackburn and Gaston, 1996; Maurer, 1999; for other taxa: Willis 1922; Rapoport, 1982; Roy et al., 1995; Hecnar, 1999) and for paleontological ones (e.g. Jablonski, 1986 and 1987; Jablonski and Valentine, 1990; Roy, 1994).

As regards the explanations for these pattern it is important to say that, at the local scale, the number of species recorded in a particular sampling area mainly depends on the pattern of the range sizes in the regional pool. At this scale of research both the presence of vagrants and the uniformity characteristics of habitats may contribute to the relatively increase in the frequency of smaller geographical ranges. At the largest spatial scale the distribution of range sizes can be determined by patterns of speciation and extinction. Species with larger ranges may be able to utilize a wide range of resources or they simply utilize wider distributed resources.

2.1.4.2 The hereditability of the range size

In 1987, David Jablonski presented a work on Cretaceus marine molluscs providing as results a strong correlation between the range sizes of sister species (or of ancestor-descendant species couples). As discussed above, the range size distribution are skewed in most cases and the log transformed data also proved skewed. The data used by Jablonski suffered of this skewness and their non-normality forced the author to use non parametric statistics to analyse them. The results of these tests affirmed the hereditability of range size and were cited as examples of species-level selection, that is to say as a property that allows the differential survivorship of a whole species and not of an individual alone as in the Darwinian natural selection theory. In 2003, Thomas J. Webb and Kevin J. Gaston presented a study where they confuted the results of

Jablonski stating that the non-parametric statistics performed on Cretaceus marine mollusc were strongly influenced by the skewed nature of the data. They performed new techniques to test the hereditability of range size using both Jablonski's data and measures of the range size of 103 living bird species. They built an index called Asy, indicating the degree of dissimilarity between sister species. For each pairs of species, Asy was computed by the difference between 1 and the ratio between the smaller (S) and the greater (B) geographic range size. After computing the Asy for all the species they compared them with a simulated sample indexes. These latter were computed on the assumption that in two sister species the smaller range size is a random portion of the larger. In other words for each value of B, S has a uniform distribution from 0 to B. The authors demonstrated that with their method there was no hereditability in the range size analysed (although they demonstrated a very weak degree of hereditability within living birds). Later, in 2005, Hunt and his collaborators presented a study in which they reaffirmed the hereditability of the range size in the Jablonski's data and in the avian data provided by Webb and Gaston (2003). They spoke out the method used by Webb and Gaston stating that the Asy was a robust index for measuring the asymmetry of range size but that the simulated model was based on erroneous assumptions. At first, they claimed that to compute simulated Asy, the measure of the smaller areas (S) should not be considered random values sampled from 0 to the values of the relative larger ones (B). Indeed, this methodology constraints S not to be independent and coming from a normal distribution. In other words S can be expected to be uniformly distributed from 1 to B only when range sizes themselves are uniformly distributed and this is not the case for the data analysed. Hunt et al., 2005 used the same Asy index computed by Webb and Gaston and showed the results coming from different assumptions regarding the distribution of B values. These simulated scenarios are based on uniform, right skewed and symmetric distributions, respectively. In all simulations the range sizes were sampled independently from the appropriate distribution. In their results, when the geographic ranges are supposed to be uniformly distributed, they got the same results obtained by Webb and Gaston with no proof for hereditability of range sizes. In the right skewed distribution scenario the results provided asymmetry values that are greater than the expected Asy showing that the range size between sister species are more different than the expected. When the simulated data were drawn by a normal distribution, the results provided a totally

different pattern with the most computed asymmetries being lower of the expected. These study provided the proof that the method used by Webb and Gaston provides different results if different assumptions are taken.

In their study, Hunt et al. (2005) stated that any simulated model should be free from assumptions. Indeed, they simply performed a randomization test shuffling the range sizes of the ancestral (or descendant) species to "destroy" any similarity due to hereditability but preserving the skewnees of the data. Then they compared the Sperman's rank correlation coefficient (r_s) of the raw data between the rs of the simulated data. They obtained that the observed rs for the Cretaceus marine mollusks was greater than all the computed 10.000 Sperman's rank correlation coefficient for simulated data (p<0.0001), thereby reaffirming the hereditability of the range sizes.

2.1.5 The inclusion of phylogenetic information in comparative studies

The acquisition of a large amount of data about extant and extinct taxa phylogenies have allowed the rising of new comparative studies largely employed to explore biological relationships and evolutionary patterns. Data acquired concern morphological, physiological and behavioural expects of the taxa, including continuous, nominal and discrete data. In the past years many studies dealt with comparative analyses leading to very important results as the relationship between the basal metabolic rate and the body mass, the "mouse-to-elephant curve" (Kleiber, 1932; Brody, 1945). Results of this kind are based on the incorrect assumption that data analyzed are independent observations (Garland et al., 2005). These studies didn't take into account the factor of the similarity of traits between phylogenetically related taxa that can lead to misleading interpretation of the results and an erroneous computation of type I and type II errors (see below).

In the second half of the last century some studies put in evidence the phylogenetic issue when comparing different taxa such as the comparisons between marsupial and placental mammals (MacMillen and Nelson, 1969; Dawson and Hulbert, 1970) and between passerine and non passerine birds (Lasiewski and Dawson, 1967), while some authors tried to partition the effect of phylogeny on physiological relationships (Andrews and Pough, 1985). The problem of including the phylogenetic information in comparative data studies was coped for the first time in 1985 by two authors independently, Felsenstein and Cheverud. In a paper published on "The American

Naturalist", Felsenstein showed the focal problem arising when the phylogeny wasn't took into account. Indeed, when we, for example, perform a simple linear regression, using two variables belonging to different taxa, we assume that any single value of the variables are drawn from a normal distribution, thereby supposing that these values are independent from each other. This is the case if we assume all taxa to belong to a phylogenetic tree in which each taxon radiated from the common ancestor simultaneously, then accumulating a certain degree of diversification. If this is the case, the evolution along any lineage is independent and the changes in the two characters (the two analysed variables) are drawn from a bivariate normal distribution and we can assume that all the conditions to perform the statistical analysis are held (Felsenstein, 1985). This particular conditions verifies in the case of a "star phylogeny" that resulted from a single explosive adaptive radiation as shown in Figure 2.2. In a star phylogeny there is no phylogenetic signal in the data analyzed and conventional statistical methods can be employed.

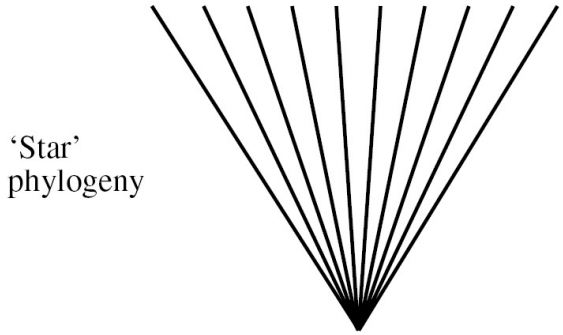


Figure 2.2 Graphical representation of a star phylogeny

There is a very low chance that the phylogenetic relationships between taxa could be drawn as a star phylogeny (Felsenstein, 1985). In nature the phylogenetic trees are more complex and sister taxa tend to resemble each other for many aspects of their phenotype (Blomberg et al., 2003). Hummingbirds look like hummingbirds, and turtles look like turtles, and the same is true for physiological traits (Blomberg et al., 2003; Garland et al., 2005). This general tendency is the natural consequence of biological contingency (Harvey and Pagel, 1991), including time lags for change to occur after speciation, occupation of similar niches by close relatives, and conservative phenotype-dependent responses to selection (Garland et al., 2005). This phylogeny-linked resemblance is named "phylogenetic signal" and the importance to include it in

comparative studies was made explicit in studies such as Freckleton et al. (2002), where in 88% of the phylogenies analyzed, at least one character showed a strong phylogenetic correlation, or in Blomberg et al. (2003), in which the phylogenetic signal was tested in 119 traits associated with 34 different phylogenies. Thus the real trees are more complex than a star phylogeny and traits are not random sample coming from a normal distribution, thereby conventional statistical methods are not suited for detect any pattern in comparative studies (Ridley, 1983; Felsenstein, 1985; Grafen, 1989; Harvey and Pagel 1991; Garland et al., 1993, 1999; Reynolds and Lee, 1996; Martins and Hansen, 1997; Ackerly, 2000; Rohlf, 2001; Swiderski, 2001, Blomberg and Garland, 2002; Garland et al., 2005; Freckleton et al., 2002; Blomberg et al., 2003; Lavin et al., 2008; Revell et al., 2008).

During the last two decades there was an increasing interest in the use of phylogeny to control for the independence of data, mainly due to the increase in advances in phylogenetic relationships reconstruction. This led to the formulation of many statistical methods to combine reconstructed trees and the data to be analyzed. Sanford et al. (2002) suggest that this new emphasis to be termed the '*comparative phylogenetic method*".

Blomberg and Garland (2002) and Garland et al. (2005) advocated this revolution in comparative studies was supported by few but strong theoretic insight such as that adaptation should not be casually inferred from comparative data; the phylogenetic information increases both quality and the type the of inferences from comparative data; as considered above, taxa cannot be assumed to be independent from each other for statistical analyses as they are differently phylogenetically related; phylogenetically corrected statistical analyses must assume some model for character evolution; taxa to be analyzed in such analyses must be chosen in regard to their phylogenetic affinities as well as the area of functional investigation; phylogenetically correct comparisons are purely correlational and inferences of causation drawn from them can be enhanced by other approaches.

2.1.5.1 The structures of a phylogenetic tree and its properties

A phylogenetic tree is the graphical representation of the phylogenetic relationships between taxa based on data provided by molecular or taxonomical informations. A phylogenetic tree must show the relationships in a monophyletic clade and can represent only the phylogenetic relationships (cladogram) or includes the information about time of divergence (phylogram). In a phylogram the hierarchical structure is based on some elements: the root, the starting point of a tree that can have a proper length; the branches which have lengths proportional to the temporal distance of the taxa or nodes from the root; the node joining two taxa; the tips, the terminals of a tree that represent the finest level of classification. When a node joins more than two taxa we have a polytomy, a condition determined by a low resolution in evolutionary information.
A phylogenetic tree can be converted in a matrix based on the information on nodes and branch lengths. In this matrix the rows and columns labels represents the tips. The diagonal values of the matrix are the distance of the tips from the root (all the same if only extant taxa are considered), while the off-diagonal represent the time of co-evolution of two taxa (actually the age of their most recent common ancestor). The diagonal values represent the variance of the matrix, while the off-diagonals the covariances. In this shape the phylogenetic information can be used in hypotheses testing (se section 2.5 for futher explanations).

2.1.5.2 The Brownian motion model

Every dissertation on the influence of the complexity of a tree on the results of a comparative study cannot be made before considering how the traits can vary along a lineage. Then it is important to introduce some models for character evolution. Any phylogenetic comparative method is based on an algorithm that includes the comparison of the variance of the measured trait along taxa with the one computed according to an expected model for character evolution.
Brownian motion is a model based on the random diffusion of a particle in a fluid driven by thermodynamic energy and has been long used for the description of continuous characters evolution (Cavalli-Sforza and Edwards, 1967; Felsenstein, 1985; 1988). This model is appropriate for evolutionary processes under genetic drift and some types of

natural selection (Felsenstein, 1988, 2004; reviewed in O'Meara et al., 2006; Revell and Harmon, 2008). In a Brownian motion model the expected character difference at any node position is assumed to be zero. According to this model, the variance of the character is normally distributed and is proportional to the distance of the node from the root. As the variance is proportional to branch length, this leads to the changes of the character values can be intense after long branches and very small after short braches. As any internal node of a tree is shorter than the tip's distance from the root, then a natural conclusion of these assumptions is that taxa that share less (external) node are more similar to each other than those sharing more (internal) ones.

2.1.5.3 The Ornstein-Uhlenbeck process (OU) and the accelerating and decelerating Brownian evolution (ACDC)

The Ornstein-Uhlenbeck process (OU) was defined by Uhlenbeck and Ornstein (data) to describe a phenomenon of a linear pressure on an entity determining its return to a central point. The linear pressure always pulls the entity toward the central point at a rate proportional to the distance between the entity and the point. This means that the expected position of the entity is in the central point. The description of this process involves spatial terms as it was formulated to describe the motion of a particle. In details, this particle moves randomly but its velocity always tends to be reset to zero by a friction. This process was invocated to dscribe a population that moves forth and back on a selective peak under the influence of genetic drift, thereby subjected to a stabilizing selection (Felselstein, 1988). In the phylogenetic comparative methods this process is used as a character evolution model as alternative to Brwnian random walk. A feature that characterizes the OU model of character change is that species'position on a character scale depends only on the recent variations and not to the position of the taxon along the phylogenetic tree. This means that this model of character evolution "forgets" past history and represents the most important difference between the OU model and the Brownian one, as in this latter the variance of the trait values is proportional to the brench length (i.e the distance in age between a node in the tree and the root). In conclusion, the feature of the OU process determines that the character evolving according to this model can show an amount of phylogenetic signal that is lower than expected from a given topology and branch lengths (Blomberg et al., 2003).

The accelerating and decelerating Brownian evolution (ACDC) was proposed by Blomberg et al. (2003) to describe the case in which the rate of evolution of a character can be subjected to variation. The ACDC model introduces a value that describes the rate at which a trait evolves. The variance of the rate of evolution changes through time. Blomberg et al. (2003) introduced a term (*g*) in the evolutionary change rate's variance that describes if the character evolution accelerates or decelerates. The term *g* is equal for each lineage, thereby in each momento at the same point in the phylogenetic tree all the lineages have the same rate of character evolution.

2.1.5.4 Phylogenetic influence on type I and II error estimations

Hypotheses testing often make use of statistical tests. When performing an experiment it is important to set a starting hypothesis (the null hypothesis, H_0) that the statistical tests have to confirm or to confute. To this aim it is important to have the probability value of occurrence of the computed results. This probability value can be obtained by experimental tables of by computer simulations. At this point there is the need to set a critical value for the probability according to which it is possible to evaluate the probability of the performed experiment. Conventionally, the probability value (level of significance, α) under which there is the rejection of the null hypothesis is set to 0.5, less frequently 0.1. Occasionally a true null hypothesis can be rejected, and in this case it is obvious that an error was committed (Zar, 1984). This error has a probability to occur tha is just the value of α. The rejection of a null hypothesis when it is true is called *Type I error* (*α error*), whereas the non-rejection of a false H0 is defined *Type II error* (β *error*).

In Garland et al. (2005) computer simulations showed what is the probability to commit a *Type I error* when ignoring the phylogenetic non-independence between the traits' values of the tree tips. The case study regards the distributions of ordinary, non-phylogenetic, Pearson product-moment correlations of tip data in order to estimate the significance of this statistics. As shown in Figure 2.3 (borrowed by Garland et al., 2005) we can see three different cases: the first, where the simulations refers to the distribution of the statistics computed according the correlation between two traits in a "star phylogeny"; the second case, in which the same simulations produced the Pearson product-moment correlations distribution related to a more hierarchical relationship

between taxa; the third, where the simulations were performed over a more real and complex phylogenetic tree. In the Figure 2.3a, b, c are reported the computed 95% and the relative conventional one-tailed critical value taken from a conventional table for correlation coefficients when all the statistical fundamental assumption are held. In each case the simulations were performed imposing to the software to follow a simple Brownian motion random walk for character evolution. In the Figure 2.3a we can see that the computed and theoretical critical value aren't statistically distinguishable as the simulations produce a typical normal (Gaussian) frequency distribution of values when a "star phylogeny" was used. This happens because in this case, as reported above, the independence of trait values was held. In the second case (Figure 2.3b) with a more hierarchical relationship between taxa, the difference between computed and theoretical critical values are significant and one can consider the statistics significant when it is not. The worst case is shown in Figure 2.3c where a more realistic phylogenetic relationship between considered taxa can lead to a stronger mislead in interpreting the results.

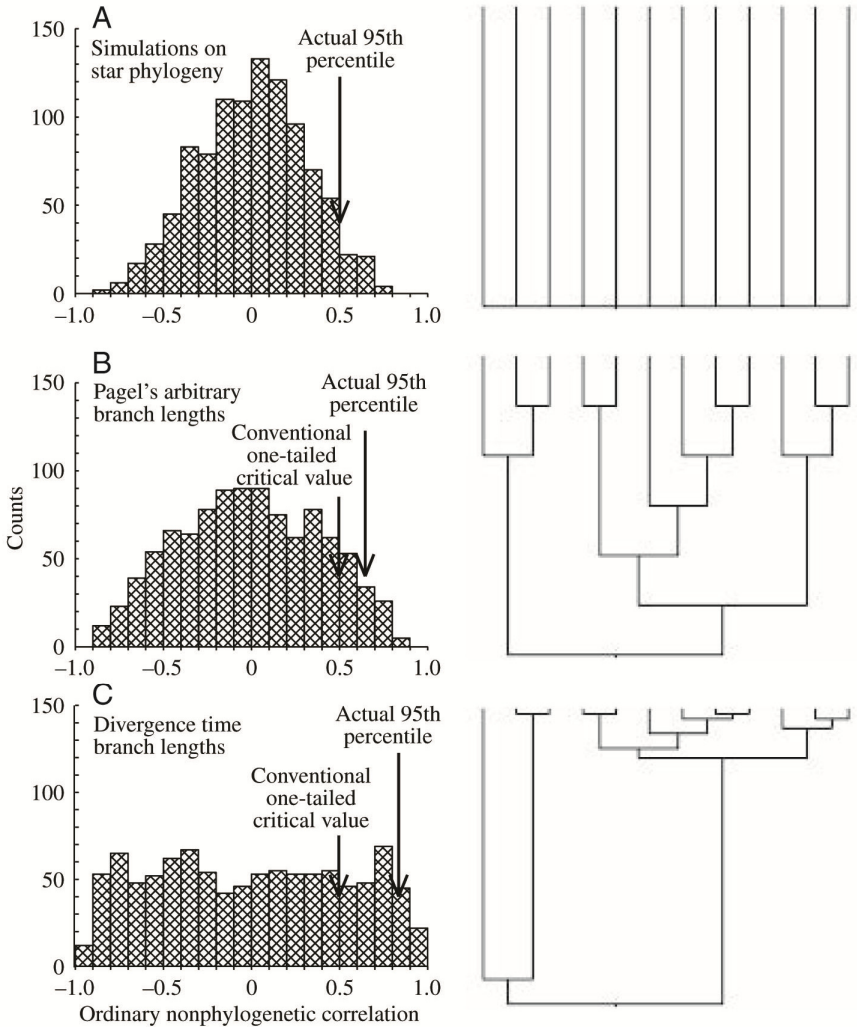


Figure 2.3

2.1.6 Phylogenetic comparative methods

2.1.6.1 Independent contrasts

As said above, Felsenstein, in his paper in 1985 ,proposed the first method to correct the statistical analyses for phylogenetical bias. He called this method independent contrasts (IC) that is based on the assumption of a Brownian motion model for character evolution. As already said, this model for evolution, based on the movement of a particle

under thermal influence, has as assumption that at any stage the expected mean value cross the whole tree is equal to zero and that the variance of the values is proportional to the distance from the root node. This latter led Felselstein to consider the branch lengths as a good approximation for trait values expected variances and to include them in traits' properties. As in each lineage the Brownian motion model is independent from the others, he assumed that the differences (the "contrasts") between two sister taxa represent independent values from the other couples. In practice he got around the problem of the dependence between sister traxa trait values computing a mean standardized value that represented the couple. He conceived the following algorithm:
Given X a trait to analyze, given X_A and X_B the trait values of the species A and B; v_A and v_B the distances (branch lengths) of the species A and B from the shared node:

1) Compute the contrast between A and B ($X_A - X_B$)
2) Divide the contrast by its standard deviation $s_x(v_A + v_B)$ computed as RadQ($v_A + v_B$) to standardize the contrast to the unitary variance
3) Repeat the previous procedures for each node.

If we consider Figure 2.4a borrowed by Garland et al., 2005, considering the 5 species we have compute 5-1 contrasts, one for each node: A – B, C – D, node 4 – node 3, node 2 – E.

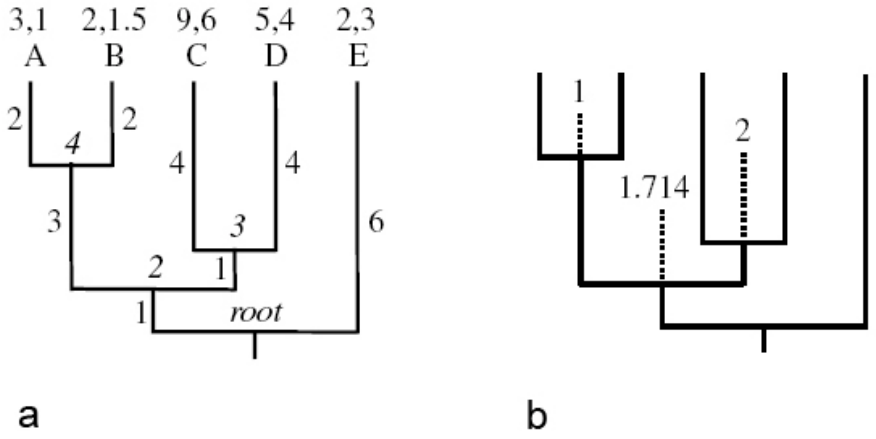


Figure 2.4

This algorithm involves the computation of contrasts between the trait values at nodes that generally are unknown. Felselstein always assuming a Brownian motion model for character evolution, proposed to calculate these values with the following expression:

$$X_k = [(1/v_i)X_i + (1/v_j)X_j]/\ 1/v_i + 1/v_J \qquad 2.1$$

Where k is an internal node and I and j are the relative sister species. In keeping with the Figure 2.4a, k could be represented by the node 4 and I and j by the species A and B. The expression y.1 only represents an estimation of trait value in internal node, not the actual one, then we have to devalue it by lengthening its relative branch (Felselstain, 1985, Garland et al., 2005). As explained in Felselstein, 1985, under Brownian motion, the amount of lengthening is computed as: (daughter branch length 1 X daughter branch length 2) / (daughter branch length 1 + daughter branch length 2). A lengthening example is reported in Figure 2.4b where nodes 2, 3 and 4 reported the values computed in the example of the Appendix in Garland et al. (2005).

2.1.6.2 Detecting the phylogenetic signal: the K statistics

A primary approach to analyze the character evolution could be to test if the distribution of the trait values on the tips of a phylogeny is different from a random one. As done in Blomberg et al. (2003), it is possible to compute the probability that a trait distribution is random by comparing it with a large set of random computer permutations of the trait values along the tips of the phylogeny considered. Random permutations allow to draw a gaussian probability distribution of trait configuration along tips by which it is possible to know the *p* value of the real trait distribution.

This approach can tell us only if the trait distribution differs from a random one but cannot give no other information on which pattern this distribution follows.

Blomberg et al., 2003 proposed a new statistics, *K*, to detect if a trait distribution along a phylogeny follows a Brownian random walk. The *K* statistics quantifies the strength of the phylogenetic signal in the trait values comparing them with an analytical expectation based on the structure of the tree and a Brownian motion model character evolution.

Then,

$$K = \text{observed}(MSE_0/MSE)/\text{expected}(MSE_0/MSE) \qquad 2.2$$

We can distinguish two terms: a ratio between observed values and ratio between expected values. As regards the first term, MSE_0 is defined the phylogenetically correct

mean, while the MSE is the mean squared error of the data computed using the variance covariance matrix derived from the candidate tree.
In detail:

$$MSE_0 = (X-a\hat{})'(X-a\hat{})/n-1 \qquad 2.3$$

Where X is the matrix containing *n* values; $a\hat{}$ is the estimation of the character value at the root node, see Garland and Diaz-Uriarte, 1999); *n* number of the tips. As we can see the MSE_0 represents quantifies the shift of the mean values of traits from the root value.
While:

$$MSE = (U-a\hat{})'(U-a\hat{})/n-1 \qquad 2.4$$

where U = DX and DX is the transformed X vector using the generalized least-squares procedure. The matrix D satisfies the equation: DVD' = I, where V is the variance-covariance matrix and I is the identity matrix (Garland and Diaz-Uriarte, 1999); $a\hat{}$ is the same as in MSE_0.
MSE_0 measures the degree of covariance within the tip data according to the candidate tree, while the MSE measures how much the structure of the candidate tree doesn't explain the variance-covariance between tip data. According to these considerations if the ration between MSE_0 and MSE is relatively high, then there is a strong phylogenetic signal while relative lower values indicate that character evolution along the considered phylogeny did not follow a Brownian random walk.
As regards the second term of equation 2.2 it is important to say that Blomberg et al. (2003) found that the computed MSE_0/MSE ratio that expresses the strength of the phylogenetic signal is strongly influenced by the complexity of the phylogeny and by the number of tips. Thereby ratios coming from different phylogenies could not be compared. Blomberg et al., 2003 proposed to introduce a second term to standardize the value of the phylogenetic signal. They introduced the ratio:

$$expected(MSE_0/MSE) \qquad 2.5$$

that represents the expected value of the phylogenetic signal under perfectly fitted Brownian motion model. If computed by equation 2.2 *K* values coming from different

phylogenies can be compared. In general a *K* value equal to 1 indicate that the trait considered has a character evolution in the candidate tree perfectly fits a Brownian motion model, while a *K* value equal to 0 representa random character evolution. A *K* value equal to 0.5 doesn't indicate that the character evolution followed a Brownian motion model and a random one but that probably the character evolution doesn't fit well a Brownian motion model. Garland and Diaz-Uriarte (1999) cautioned to use in addition to *K* other models that are based on different assumptions (such as the Ornstein-Uhlenbeck or ACDC models).

2.1.6.3 Pagel's λ

Another statistic parameter useful to test for the phylogenetic signal in the measured traits of taxa is *Pagel's λ* (Pagel, 1999). *Λ* is defined as a multiplier of the off-diagonal elements of the variance-covariance matrix (Pagel, 1999). This statistics is estimated by a Maximum Likelihood method, in which the observed data on taxa and the model of character evolution are represented in a common probabilistic framework (Pagel, 1999). Indeed, given the particular model of evolution of the Brownian random walk, the Maximum Likelihood method seeks to compute the most probable parameter that best describes the observed data. Form the mathematical perspective, *λ* modifies the branch lengths in the way that trait's values at the tips are those expected by a Brownian motion model character evolution. This statistics can vary between 0 and and a value that can be greater than 1. If *λ* has a value equals to 0 then it implies that the evolution of the traits is independent of phylogeny, while a value equals to 1 suggests that the traits evolved according to a Brownian motion model and, thereby there is no modification of the branch lengths . Values comprised between 0 and 1 indicate that the evolution of the traits occurred with an influence of the phylogeny that is weaker than it happens in a Brownian Random Walk (Freckleton et al., 2002). *Λ* is quite different from other statistics such as k (Blomberg et al., 2003) or H^2 of the Lynch's model (Lynch, 1991) as it can have values greater than 1. Indeed, as regards, for example, the Lynch's model, H^2 is a value represented by the ratio between the supposed phylogenetic and non phylogenetic compotents of the data and, thereby, this ratio cannot be greater than 1. Instead, *λ* maximizes the fits of the whole unpartitioned data to a Brownian motion model. Then, this statistics can show value greater than 1 if, for instance, traits between

sister taxa are more similar than expected by the supposed Brownian evolutionary model (Freckleton et al., 2002). It is worth to say that the λ' values are finite as the off-diagonal elements can't be greater than the diagonal ones (Freckleton et al., 2002).
Further explanations about the computation of both λ and K will be provided in the relative section of the material and methods paragraph.

2.2 Materials and methods

2.2.1 Taxa occurrences and age estimation

The analyses presented here are employed using the species' occurrences database presented in the previous chapter. For the proposed hypotheses testing the database was reduced from 782 to 690 Local Faunal Assemblages (LFAs) of Western Eurasia as for the removal of the LFAs not belonging to any EAPCOMs as a warranty of the correct link between the similarity of taxon lists and similar age estimations of the LFAs. As the removed localities were not located at the temporal boundaries of the whole database, this latter preserves its duration spanning in time from the Middle Pliocene to the Early Holocene. The removal of the localities implied the reduction of the species considered from 220 to 163.
For the age estimation of the all LFAs it was used the arithmetical mean between the Fidler Scores and the MLAEO Scores computed for each LFA in the chapter 1. This means well correlate with chronological age as shown in Figure 2.5. Then the function expressing this correlation was used to estimate the age of the localities without any age data. Finally we used both these computed ages and the radiometric or paleomagnetic ones where available for the following statistical analyses. The Appendix B reports all the LFAs used for this study and the relative geographical coordinates and age estimates.

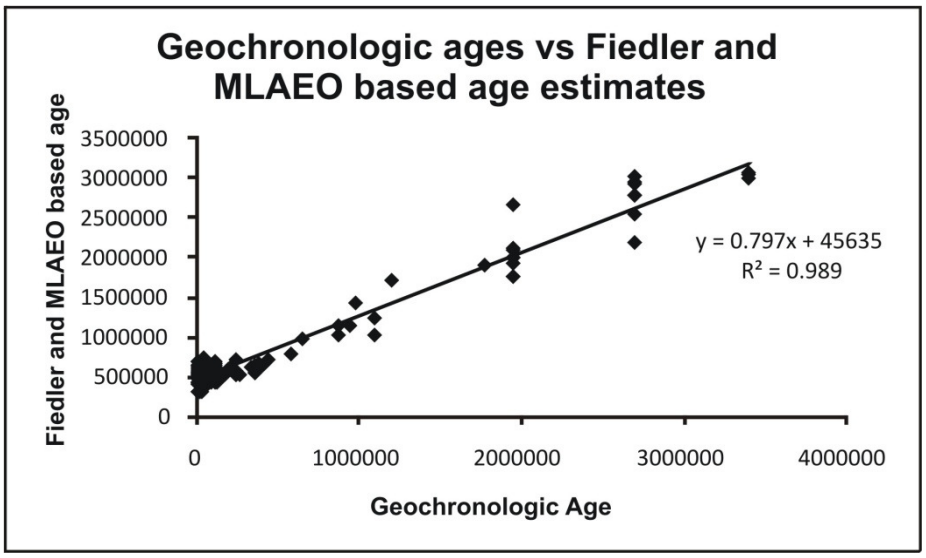


Figure. 2.5 Correlation between the geochronologic ages and the ages over the arithmetical means between Fiedler and ML AEO estimates

2.2.2 Body size and duration

The species body sizes included in the statistical analyses were taken from the data provided by Meloro et al., (2007). The computation of the genus body size estimates was performed by the arithmetic mean of the body size measures of all the species comprised in a particular genus included in the occurrences' database.

As regards the taxa durations, their estimates were computed by the difference between the taxon First Appearance Datum (FAD) and Last Appearance Datum (LAD). It is worth to say that these estimations are not considered as the real duration of the species or genera as a taxon differenciates, could be not so abundant to be recorded as fossil. The same can be said for a taxon near to its extinction, as it could continue to exist later than its LAD in restricted populations that are too small to overcome taphonomic bias. Then, the computed durations are considered here as a simply estimates of the persistence of the taxa to made possible the performing of the comparative analyses.

2.2.3 Species level and genus level phylogenies

For the phylogenetic comparative methods employed in this chapter, the phylogenies and relative branch lengths were prepared borrowing the data from Raia, P. (in submission). These phylogenies will be shortly discussed here. Both for species and genera taxonomic level of analyses, two different phylogenies were build that comprise the living and fossil mammals considered in these chapter.

The first tree takes into account the question about the monophyly of the Artiodactyla (Price et al. 2005). Indeed, molecular studies place hippopotamuses together with cetaceans, while older accounts, based on morphology, recognize a clade including hippos, peccaries and pigs. Cladistic analyses performed by Geisler and Uhen (2005) took into account morphological and molecular data and their results supported the creation of the "whippomorpha" (hippos+whales) clade, the monophyly of Tylopoda, and a 39 My long gap in the fossil record of Hippopotamidae (see also Theodor, 2004). See the Appendix D for a graphical representation of the discussed phylogeny 1.

The second phylogeny consider the question of the uncertainty of the monophyly of Ungulata as suggested by Janis (2008). According to Waddell et al. (1999), ungulates and carnivores are located in the clade Ferungulata, together with Pholidota, with Perissodactyla standing closer to Carnivora than to Cetartiodactyla (Springer et al., 2005). This second tree differs from the first for the placement of Irish elk and related taxa (megacerine deer). In this tree *Megaloceros giganteus* and its close *Megaloceros savini* are considered as sister taxa to *Cervus*. Indeed, a recent study based on both mtDNA and cytochrome b gene found a red deer-*Megaloceros* relationship (Kuehn et al., 2005), in keeping with the results of a cladistic analysis of post-cranial elements of cervine deer (Pfeiffer, 1999).

For both the trees most fossil taxa were considered as soft polytomies within genera, unless alternative and little disputed phylogenetic opinions were available in literature (e.g. the close relationship between cave bears *U. deningeri* and *U. spelaeus*).

An important characteristic of both the discussed trees is that they are not ultrametric, meaning that the terminal date for each species is represented by its last occurrence in the fossil record.

According to the data borrowed from Raia, in submission, the topology and branch lengths for ruminants follow the informations provided by Hernández Fernández and Vrba (2005), while the phylogeny of carnivores are built on the data of Bininda Edmons

et al. (1999). The phylogenetic relationships for non-ruminant ungulates and divergence date estimates among orders were taken by Cao et al. (2000) and Bininda Edmons et al. (2007). As regards the extinct species, the specialistic papers were examined to draw their phylogeny. In particular, the topology for fossil Bovinae follows the data provided by Geraads (1992) and Brugal and Croitor (2004). The megacerine deer tree topology is built on the phylogeny presented in Croitor (2004), while the Irish elk *Megaloceros giganteus* was positioned outside the megacerines and close to the fallow deer, according to Lister et al. (2005).

The data of Cerdeño (1995) and Lacombat (2006) were used to draw the phylogeny of fossil rhinos. As there is no consistent phylogeny for the species included in the genus *Equus*, these are included in the tree as an unresolved clade containing a (soft) polytomous clade of stenonian horses, plus a clade containing the hemione and the hydruntine horse *E. hydruntinus*, and separately *Equus ferus*, in keeping with Alberdi et al. (1998).

As regards the fossil bears, the phylogenies presented here is built on the hypothesis suggested in Mazza and Rustioni (1994). The phylogenies of machairodont cats and canids follow Slater and Van Valkenburgh (2008), and Wang (2004) respectively, while the taxonomy and phylogeny of hyenas follows the information provided by Werdelin and Solounias (1991). For elephants the taxonomy and phylogeny follow Shoshani and Tassy (2005), while the divergence dates within this clade were taken from Thomas et al. (2000). All the remaining divergence estimates were taken from the paleobiology database (http://paleodb.org/cgi-bin/bridge.pl) and from the NOW database (http://www.helsinki.fi/science/now/).

2.2.4 Geographical distances between taxa

Every species and genus was geographically localized by a single point, useful for calculating geographical distances between the taxa. To do this in ArcGis 9.2 it was used the tool “Central Feature” as an estimation of the taxon position. The central feature was chosen to identify the position of the taxon because it provides a combination of geographical coordinates that matches with an effectively existing locality of the sample in which the particular taxon was found. Indeed, for a particular taxon, it provides the most central locality that has the minimum distance from all others

in the same sample. The geometric centre, that is the centre of the minimum convex polygon identified by taxon localities, was not used here as it could provide a wrong information because of the geographic coordinates computed don't take into account of the spatial distribution of localities. In addition, sometimes, the geometric centre could be in a position not coherent with taxon's biology or ecology, as it could be localized in the sea surfaces or lakes. For the estimation of the central feature we used the euclidean distance computation. Then the distance matrix between localities was build over these data using the Hawth Tolls for ArcGis 9.2. This matrix was used to estimate if phylogenetic closely related taxa were geographically closer than at chance. Phylogenetically close taxa are defined as taxa with a patristic distance of 1 node (sister taxa). This assumption is restricted to only the analysis at the species level because, at the genus level, the species included may not be separated by only one patristic distance. Then, for genera, the node count distances should not be limited to 1, but to the aim of these analyses, only the results related to one patristic node distances will be shown and discussed.

To this aim the first step was the computation of the average distance between sister taxa central features. Then these taxa were removed from the original distance matrix. The following step was to simulate 10,000 random vectors of pairwise distances between taxa with a patristic distance greater than 1. The null hypothesis of this test is that all the simulated distances are equal or smaller than those computed for the closely related taxa. If this null hypothesis is rejected, sister taxa tend to occupy closer than expected ranges. Consequently, genera range sizes must be smaller than the raw sum of their constituent species range sizes. These procedures were applied for both species and genera geographic ranges.

2.2.5 Occupancy computation and trajectory

In the occupancy calculation we only considered taxa belonging to the computed EAPCOMs with a minimum of 10 occurrences. For occupancy trajectory drawing, for each taxon, the time span embraced by the sample of the localities was divided into 5 temporal slices of equal time interval. Then we only considered taxa for which there were possible to calculate 3 time slices at least. For this reason the total sample of species was reduced to 54 and the sample of genera was reduced to a number of 20.

Because of the inconstancy of fossil data, sometimes it was not possible having temporal slice of the estimated time interval. In this case subsequent time slices were collapsed. For this reason, in no case it was possible to have five temporal slices. As for the data considered span over a very long time interval, for every time slice there is a different sampling bias. For this reason the estimation of the occupancy was given by an index computed by dividing the number of localities were species occurred (LOCS) of every temporal slice with the number of all localities sampled (LOCTI) belonging to EAPCOMs and comprised in the slice's time boundaries. For each slice the ratio (LOCS/LOCTI) represents the occupancy computed for that time interval. Then the lower boundary of a time slice was divided by the duration of the particular taxon (the age of the First Appearance minus the Last Appearance in the EAPCOM system) and this ratio was used to determine the position of a time slice within the identified chronological boundary of the particular taxon duration.

For each taxa the occupancy maximum and the mean averaged over all time-slices, and the value at the first time slice were computed. Finally, a general descriptive model was drawn using all the occupancy values and time slices for all taxa collated in chronological order.

The method described below is the most conservative and parsimonious one to draw an occupancy trajectory build over at least three time slices per taxon.

2.2.6 Geographic range computation and its trajectory

The geographic range of a taxon is considered here as the area of the surface of the minimum convex polygon delimited by taxon's occurrences. Actually there is a dispute in discriminating between the extent of the occurrence and the area of occupancy (Gaston and Blackburn, 2000). The former is defined as the outermost limits to the occurrences of a species while the latter is defined as the area (surface) over which it is actually found (Gaston 1991c, 1994). The computation of the range size performed in this doctoral thesis is, in its first stage, closer to the definition of the extent of occurrence. To have a proxy of the area of occupancy, the polygon describing the range size of a taxon was subsequently corrected by the elimination of portions not coherent with the supposed taxon ecology (see below for further explanations).

The computation of the areas was performed over the polygon delimited by the localities comprised in each time slices created for the computation of occupancy trajectory. As for the occupancy, the area is represented by an index . This is the ratio between the area of the surface delimited by the localities (A-LOCS) recording a specific taxon and the area of the surface delimited by all the localities (A-LOCTI) belonging to EAPCOMs and included within taxon's FA and LA. For these computations only time slices including at least three localities were used, as this is the minimum number of items to draw surfaces of which calculating area. In ArcGis 9.2 all the data were analysed using the Lambert Azimuthal Equal Area Projection. For each taxon, the geographical coordinates of the localities within a time slice were used to draw a minimum convex polygon. As discussed above, the computation of the area of this kind of polygon may be erroneous because the polygons built over the distribution of taxa often include sea portions, lakes or island not really inhabited by the specific taxa. For this reason a new shapefile containing sea surface and islands was created to be used to erase surfaces incoherent with taxon ecology and occurrences. After these surface corrections the areas were computed. This correction was the attempt to obtain a range size that is the closest proxy to the definition of the area of occupancy. Each area has a temporal position along the taxon's duration that is the same of the belonging time slice.
As for occupancy, the maximum, the arithmetical mean and the starting areas were computed. Then, using the most frequent trajectories, a general descriptive model was built for range size trajectories.

2.2.7 The hereditability of the traits

After the computation of the starting, mean and maximum occupancy values and after the computation of the starting, mean and maximum areas, these traits, together with the body size and duration estimates were used for the comparative phylogenetic hypotheses testing. The analyses performed were the Phylogenetic Independent Contrasts (Felselstein, 1987) and the test for detecting the phylogenetic signal by computing both K statistics (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999; Freckleton, 2002) (see the relative section in the introduction of this chapter). All these nanlyses were performed using the "R" statistical package. In particular, the Philogenetic Independent Contrasts were computed using the "Picante" library (Kembel

et al., 2009), while both K statistics and Pagel's λ were computed by the "Gaiger" library (Harmon et al., 2008).

2.3 Results

2.3.1 Occupancy and Area trajectories

The occupancy trajectories were computed for 54 species and 20 genera (the genera used were both extinct and locally extinct, e.g *Panthera*, *Bison*, taxa) . 40 species (74% of the total) show a peaked trajectory, while 9 (17%) show a descending trajectory and 4 (7% of the total) show an ascending one. The single remaining species cannot be fitted in occupancy trajectories this simple. The Figure 2.6a shows the general model plotted using all the species with a peaked trajectory. As regards genera, 14 (70 %) show a peaked trajectory, and 2 (10 %) show ascending trajectories. Four genera 4 (20 %) have more complex trajectory shapes. The Figure 2.6b shows the general model built on genera peaked occupancy courses. In Among species, 68% of the peaked trajectories occur in herbivores, the remaining in carnivores. Among genera, the corresponding figures are 79 and 21%. Fisher's Exact Test shows that these percentages are not different by the initial proportion of herbivores and carnivores in our dataset (for species $p = 0.55$; for genera $p = 0.57$).

Only 36 out of 54 species analyzed have at least 3 time slices for which calculating areas (a time slice must include more than 2 LFAs where the species occur to get a meaningful area estimate). Fifteen of them (42 %) have a peaked area trajectory, 6 (17 %) have an ascending area trajectory, 11 (31%) show descending area trajectories, and 4 species (11 %) have more complex trajectories. For genera we could draw 17 area trajectories out of 20 taxa. Ten genera (59%) shows a peaked trajectory, while 1 (6%), 2 (12%) and 4 (23%) genera have shown ascending, descending and more complex trajectories respectively. It was not possible to draw any general model for area since, although it is the most frequent shape, the peaked trajectories represents less than the 50% of the total. In sum, for both area and occupancy a peaked trajectory is the most frequent. See Appendic C to consult all the computed measures.

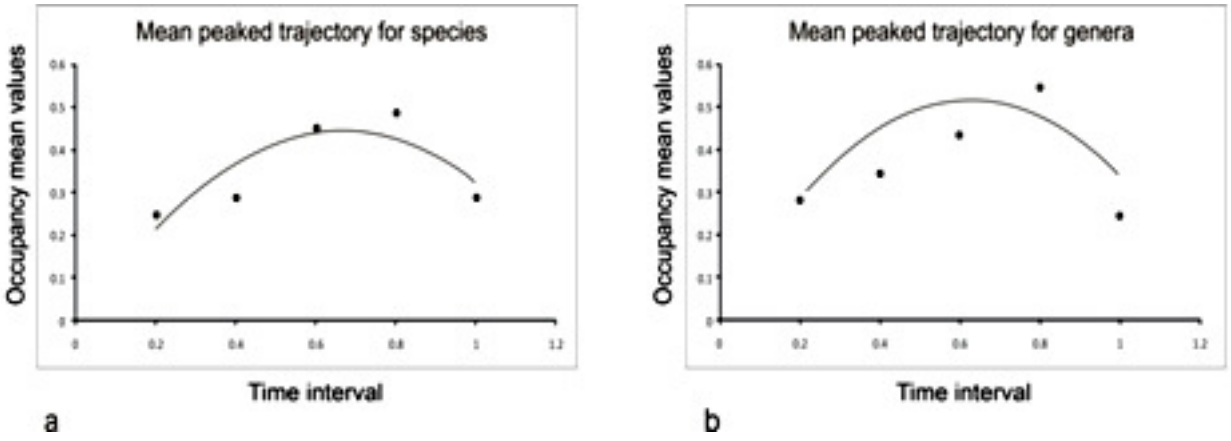


Figure. 2.6 General model for the occupancy of species (a) and genera (b)

2.3.2 Tests for phylogenetic signal and PICs correlations

Body size shows a very strong phylogenetic signal, both using K or Lambda for inferences, and regardless of whether alternative phylogenies and either species or genera are considered (Table 2.1). Duration, area and occupancy at the beginning of taxa appearance, and area and occupancy maxima show no phylogenetic signal. On the contrary, mean occupancy and mean area of genera show either significant or marginally significant phylogenetic signal, at the genus level (Table 2.1). This implies that mean occupancy and area are more variable within genera that among genera.

PICs correlations for the two species-level phylogenies and the two genus-level phylogenies are shown in Table 2.2. There is a significant correlation between estimates of area with each other, between estimates of occupancy with each other and between these two groups of variables. Though, area and occupancy at the beginning of both species and genera record tend to correlate to each other more than with other area and occupancy metrics (Table 2.2). Initial occupancy (and initial species area by using phylogeny 1) happens to correlate significantly with duration. This probably reflects an effect of sampling (ephemeral species may appear overly rare at their appearance).

Body size is significantly correlated to mean and maximum occupancy and to mean and maximum area within species, but much less so within genera (Table 2.2).

2.3.3 Range position and phylogeny

By using species-level phylogeny1 the average distance between sister taxa's central features is 467.381 Km. Random distance averages have a mean of 567.307 Km and a 5th percentile of 481.767 Km. Only 259 out of 10,000 random vectors average less than 467.381 Km ($p = 0.026$).

By using species-level phylogeny2 the average distance between sister taxa is 438.677 Km. The mean random distance is 567.299 Km, and the 5th percentile of random vector average distance is 511.573 Km. None of the random averages is as small as the real data average distance ($p < 0.001$). These results indicate a very strong tendency for sister taxa to be preferentially distributed in the same geographical territories.

Table 2.1 – Phylogenetic Signal calculated for both species and genera by using two different topologies per taxonomic level. Phylogenetic signal was calculated by using both Pagel's λ and Blomberg et al's K statistics. Significant and marginally significant (at $p < 0.1$) relationships are reported in bold face.

Phylogenetic Signal

Phylogeny Species 1	**Body_size**	**Duration**	**MeanOcc**	**MaxOcc**	**Mean Area**	**Max Area**	**Occ1**	**Area1**
Lambda	**1.000**	<0.001	0.223	0.274	0.195	0.102	0.194	<0.001
p (lambda = 0)	**0.000**	1.000	0.156	0.110	0.085	0.397	0.165	1.000
K	**0.728**	0.098	0.105	0.094	0.080	0.076	0.072	0.037
p (K = 0)	**0.001**	0.105	0.234	0.210	0.562	0.580	0.447	0.906
Phylogeny Species 2								
Lambda	**1.000**	<0.001	0.243	**0.318**	0.208	0.119	0.194	<0.001
p (lambda = 0)	**0.000**	1.000	0.130	**0.080**	0.075	0.320	0.163	1.000
K	**0.968**	0.097	**0.130**	**0.128**	0.113	0.094	0.076	0.043
p (K = 0)	**0.001**	0.230	**0.084**	**0.019**	0.212	0.406	0.530	0.891
Phylogeny Genera 1								
Lambda	**0.945**	<0.001	**0.761**	0.668	0.708	<0.001	<0.001	<0.001
p (lambda = 0)	**0.004**	1.000	**0.079**	0.299	0.144	1.000	1.000	1.000
K	**1.015**	0.294	**0.726**	**0.614**	**0.809**	0.447	0.381	0.315
p (K = 0)	**0.005**	0.594	**0.038**	**0.066**	**0.052**	0.182	0.438	0.432

Phylogeny								
Genera 2								
lambda	**0.912**	<0.001	**0.724**	0.423	0.736	<0.001	0.227	<0.001
p (lambda = 0)	**0.009**	1.000	**0.082**	0.512	0.115	1.000	0.983	1.000
K	**0.876**	0.272	**0.619**	0.431	**0.709**	0.343	0.317	0.282
p (K = 0)	**0.003**	0.558	**0.059**	0.184	**0.050**	0.345	0.453	0.404

Table 2.2 - Phylogenetic Independent Contrasts correlations. For each phylogeny, correlations are reported in the upper right corner and their significance values in the lower left corner. Significant correlations appear in bold face.

Phylogeny Species 1	**Body size**	**Duration**	**Mean Occ**	**Max Occ**	**Mean Area**	**Max Area**	**Occ1**	**Area1**
Body size	0	-0.177	**0.407**	**0.479**	**0.565**	**0.509**	0.081	0.280
Duration	0.223	0	0.216	0.153	0.052	0.130	**0.571**	**0.416**
MeanOcc	0.004	0.136	0	**0.916**	**0.541**	**0.498**	**0.380**	0.147
MaxOcc	0.000	0.295	0.000	0	**0.554**	**0.537**	**0.295**	0.138
MeanArea	0.000	0.723	0.000	0.000	0	**0.951**	0.207	**0.662**
MaxArea	0.000	0.372	0.000	0.000	0.000	0	0.263	**0.725**
Occ1	0.579	0.000	0.007	0.040	0.154	0.068	0	**0.551**
Area1	0.052	0.003	0.312	0.343	0.000	0.000	0.000	0
Phylogeny Species 2	**Body size**	**Duration**	**Mean Occ**	**Max Occ**	**Mean Area**	**Max Area**	**Occ1**	**Area1**
Body size	0	-0.270	0.149	0.220	**0.344**	**0.309**	-0.083	0.072
Duration	0.060	0	0.205	0.130	-0.007	0.103	**0.564**	0.410
MeanOcc	0.307	0.158	0	**0.882**	**0.336**	**0.310**	**0.290**	-0.057
MaxOcc	0.128	0.373	0.000	0	**0.321**	**0.339**	0.176	-0.102
MeanArea	0.016	0.962	0.018	0.0246	0	**0.931**	0.057	**0.586**
MaxArea	0.031	0.480	0.030	0.0173	0.0000	0	0.149	**0.663**
Occ1	0.570	0.000	0.043	0.227	0.698	0.305	0	**0.501**
Area1	0.622	0.003	0.695	0.485	0.000	0.000	0.000	0

Phylogeny Genera 1	**Duration**	**Mean Occ**	**Max Occ**	**Mean Area**	**Max Area**	**Body Size**	**Occ1**	**Area1**
Duration	0	0.339	-0.125	0.224	0.039	-0.088	-0.011	0.173
MeanOcc	0.133	0	0.080	0.384	0.187	0.119	0.090	0.230
MaxOcc	0.591	0.731	0	**0.509**	**0.448**	**0.524**	**0.531**	0.118
MeanArea	0.328	0.086	0.01855	0	**0.579**	0.292	**0.586**	-0.010
MaxArea	0.865	0.417	0.042	0.006	0	0.146	0.057	0.005
Body size	0.703	0.608	0.015	0.198	0.528	0	0.148	0.003
Occ1	0.963	0.698	0.013	0.005	0.806	0.523	0	0.215
Area1	0.452	0.316	0.612	0.965	0.983	0.989	0.349	0

Phylogeny Genera 2	**Duration**	**Mean Occ**	**Max Occ**	**Mean Area**	**Max Area**	**Body Size**	**Occ1**	**Area1**
Duration	0	0.064	0.085	-0.221	-0.322	-0.288	**-0.475**	0.069
MeanOcc	0.784	0	**0.875**	0.412	**0.517**	0.412	**0.468**	0.172
MaxOcc	0.714	0.000	0	0.071	0.331	0.423	0.179	-0.053
MeanArea	0.336	0.064	0.760	0	**0.817**	0.393	**0.654**	**0.601**
MaxArea	0.154	0.016	0.143	0.000	0	0.364	**0.622**	**0.507**
Body Size	0.206	0.064	0.056	0.078	0.104	0	0.180	0.199
Occ1	0.030	0.032	0.437	0.001	0.003	0.434	0	0.335
Area1	0.768	0.455	0.820	0.004	0.019	0.388	0.138	0

2.4 Discussion

Results show that seventy-four per cent of the extinct species- and 55% of the (either extinct or locally extinct) large mammal genera lived from Pliocene to Recent of Western Eurasia follow a peaked occupancy trajectory. Despite results provided in Raia et al. (2006) for quaternary fossil mammals, there are no statistical differences between herbivore and carnivore taxa in the distribution of peaked trajectories. In keeping with previous accounts dealing with Cenozoic nannoplankton, diatoms, planktic foraminifers and radiolarians (Liow and Stenseth, 2007), Cenozoic New Zealand's marine mollusks (Foote et al., 2007), Neogene mammals of Europe (Jernvall and Fortelius, 2004), large mammals from Italian Plio-Pleistocene (Raia et al., 2006), and recent birds (Webb and Gaston, 2000) the results show that the peaked trajectory is the dominant mode of occupancy evolution in our data. Thus, over a variety of temporal and geographical scales, and analyzing quite different organisms, the notion for a predominance of the peaked trajectory holds. It should probably be taken as a robust generalization, especially because a number of factors may obscure any recurrent patterns in taxa geographic evolution, including mass extinctions (Foote et al., 2007), environmental perturbations (Jenkins, 1992) and trophic level (Raia et al., 2006).

The computed results that show area trajectories to mimic occupancy's are in agreement with some authors (Gaston and Blackburn 2000; Gaston, 2003; Blackburn et al., 2004) stating that occupancy is highly correlated to range size across scales,. Peaked trajectories are still predicted by the positive effect of species duration on occupancy and vice versa (Foote, 2007; Foote et al., 2008). As regards these trajectories it is possible to discuss their starting, middle and ending values that determine this kind of shape. Low starting values are coherent with the conclusions of Vrbà and De Gusta (2004). According to these, small population sizes are the norm due to the kind of speciation (see below) and abundance is positively correlated with occupancy (Brown, 1984; Brown and Maurer, 1987; Rosenzweig, 1991; Hanski et al., 1993; Holt, 1997; Gaston and Blackburn, 2000; Harte et al., 2001). As regards the following rising values that lead to the peak, it is important to say that populations too close to their minimum-vital size generally show an increase to improve their chance of survivorship (Vrbà and De Gusta, 2004). Moreover it could be due to a sample bias because, for the fossil records considered in this doctoral thesis, there is too low

resolution sampling power to detect populations that decrease their size after a low starting one (but this is not the case for trajectories drawn with extant taxa) or because, as said above, actually, these populations have a high chance of extinction.

A descending branch cannot be drawn when a taxon is involved in mass extinction determined by very strong environmental changes. Then, the occupancy and area trajectories could undergo a truncation, leaving only the ascending branches . Still, when the environment changes gradually, local populations, if not adapted, undergo a gradually size decrement leading to extinction, or to local extinction, when a species with a high dispersal ability moves to more suitable habitat. According to Johnson, (1998), when a species is near to extinction, it becomes locally abundant but regionally uncommon or locally rare but widespread. Moreover mammal species show very low population sizes before going extinct (Brashares, 2002). All these scenarios perfectly fit with the provided results.

A different question relates to the absolute dimension of both range size and occupancy. The hereditability of range size is still a debated topic (Jablonski, 1987; Webb and Gaston, 2003; Hunt et al., 2005: Waldron, 2007 and see the relative section in the introduction of this chapter). The results provided marginal evidence that mean occupancy and area are similar between sister genera (Table 2.1). At the species level, both K and λ statistics are much lower and never significant. But it is woth to say that there is a significant correlation between estimates of area and occupancy when phylogeny is accounted for, and both kinds of estimates are highly correlated to body size (Table 2.2). Since the results show that body size has the strongest phylogenetic signal, it is conceivable that its heritability has a positive influences on both area and occupancy heritabilities. Indeed, larger species tend to have larger home ranges, dispersal ability, range size and occupancy than smaller species (Kelt and Van Vuren, 1999; Pyron, 1999, Gaston, 2003). Thereby, it could be possible that the computed mean measures of area and occupancy are probably too crude to detect any possible phylogenetic signals. Indeed, as the measures are averaged over a taxon lifetime, they colud be affected by variability in sampling intensity which is certainly present in collected data. Moreover, the arithmetic means values could not be precise representations of both range size and occupancy as these latter are known to vary over taxon life span (Foote et al. 2008).

As regards the genus level, the results provide K and λ values that are higher than those at the species level for both mean and maximum occupancy and area. These results are coherent with those showed in Waldron (2007), according to which phylogenetic signal in range size within large clades, such as marsupials, mammals and North American birds, are found to be greater than in lower taxonomic levels (Waldron, 2007).

Area and occupancy maxima and initial values, however, do not show any phylogenetic signal. Whereas different range and occupancy maxima may probably be influenced by a few, very successful species within genera, different range sizes are expected to be common for sister species when they "split" because of allopatric speciation. According to Vrba and De Gusta (2004), small and restricted populations are expected to leave their source populations because of environmental changes and to be a genetic pool for possible allopatric speciation. A similar asymmetry in the areas of sister clades is predicted to occur by the mechanism of peripatric speciation too, in which small and narrowly distributed populations, at the margins of a species area, are more likely to undergo genetic drift (Barraclough and Vogler, 2000) Yet, ranges may become more similar after the split, according to Waldron (2007). Barraclough and Vogler (2000) and Wladron (2007) simulated range motion and post-speciational range size change through time. They found that sister-species ranges tend to increase in overlap through time, even if allopatry is the dominant mode of speciation. The results I provided showed that sister-species' central features are closer than expected by chance, meaning that sister species tend to occupy the same territory (i.e. they were sympatric for some time or replaced each other physically, either). This latter finding also bears on the mechanism likely to drive range expansion at the genus level. Miller (1997) envisaged genera range expansion may be determined either by the origination of new, geographically non-overlapping, species within the genus, or by range size increase of the constituent genera. The results I provided are consistent with the latter scenario as: first, most of the congeneric taxa considered in this study lived in a temporally disjunctive (or better little overlapped) time frame, thus not determining a consistent increase of taxa during genera time span and, second, their phylogenetically conserved central features constitute the proof that they lived in the same territories. This means that the measured range expansion should be determined by the geographical enlargement of few species and not by the increase of species number.

Chapter 3 -Macroecology of the fossil mammal assemblages: the species accumulation over space and time

3.1 Introduction

The uneven distribution of species richness above the Earth has always captured the attention of every ecologist. In 1972, Robert MacArthur, after analysed the great deal of papers dealing with topic, asked if a general pattern behind all the analyzed examples really exists or these examples are all a set of case histories, each own having its explanation. Species richness is defined as the total number of species recorded in a defined area (McIntosh, 1967). The term "richness" must not be identified with the term "diversity", this latter also considering the number of individuals per species. The species richness is a measure that is strongly influenced by the scale of observation and, for this reason, this pattern is object of macroecological investigations. As stated by Gaston and Blacburn (2000), species richness measured at local scale can be considered as the smallest piece in a "Russian dell-like" set of nested faunas at the regional scale. There are many studies dealing with the effects of spatial scale on species richness (the species-area relationship, SAR) and concerning with spatial species turnover, performed on both actual and paleontological records. (for example Connor and McCoy, 1979; Rosenzweig, 1995; Rosenzweig, 1998). The species accumulation over time (the species-time relationship, STR) is, instead, a pattern less studied as for it requires the accumulation of data during increasing time periods of observation. Nevertheless, this pattern deserves an increasing interests by many researches, involving both ecologist and palaeontologists. Recently a new perspective is rising to attention of macroecologists as it allows to take into account the effects of both spatial and temporal factors on the species richness. This is the species-time-area relationship (the STAR) that was at first provided by Rosenzewig in 1998 and, then, improved by Adler and Lauenroth in 2003. The model is innovative as it provides the temporal and geographical scales at which spatial and temporal species turnover are equals, thus providing an important tool for conservationists.

The aims of this chapter are to use the Western Eurasia fossil record, discussed in the first chapter, and spanning in time since the Middle Pliocene to the Early Holocene as follows:

- To build a species-area relationship (SAR) considering different spatial sampling scales from singular equal-area cells, in a grid superimposed to the geographical territory of study, to at the scale of the whole Western Eurasia;
- To build a species-time relationship (STR) over the whole fossil records spanning in time since 3.7 Mya to 0.05 Mya;
- To build STRs models at smaller temporal scales and analyze the variation of temporal species turnover rates with climatic changes;
- To build the species-time-area relationship (STAR).

3.1.2 The species-area relationship

There is a strong relationship between species countered in a survey and the size of the sampling area. Indeed, it is possible to observe that the number of taxa sampled increases considering larger and larger sites. This is the species-area relationship and is one of the most robust pattern observed in ecology (Connor and McCoy, 1979; Williamson, 1988; Rosenzweig, 1995). The first author that formally modelled this patter was Arrhenius in 1921, and he found that this relationship could be described by the mathematical formula:

$$S = cA^z \qquad 3.1$$

Where S is the cumulative number of species (i. e. the total number of species found in any sampled area size), A is the area of the site's surface whereas z and c are constants. Arrhenius also provided the logarithmic form:

$$\text{Log}(S) = z\,\text{Log}(A) + \text{Log}(c) \qquad 3.2$$

Gleason (1922) proposed an exponential form ($S = z\,\text{Log}(A) + \text{Log}(c)$), thus opening the question on the best fit model for describing this relationship (Dony, 1970; Connor and McCoy, 1979; Stenseth, 1979; He and Legendre, 1996 ; Tjørve, 2003). Despite this question all the authors recognized the importance of what *z* represents. In the logarithmic form (3.2) it is evident that *z* represents the slope of the regression line that describes the relationship between *S* and *A*. As stated by Rosenzweig (1995), there is

not a single factor behind the z values, but this latter depends on the areas involved and by their interrelationships. *z* describes the rate by which the species number increases along with the area. According to the values of *z*, Rosenzweig (1995) recognized four types of species-area relationships (Figure 3.1). The first describing the relationship between species and area for tiny pieces of biota, whose description is outside of the macroecological context considered in the topic. Considering increasing sampling size, the following type is that describing the species-area relationships between islands in an archipelagos, showing z values ranging from 0.25 to 0.35. In this case the areas involved are not nested and each island is a sampling site. Plotting the pattern across different areas within a whole province provides lower values of z ranging from 0.12 and 0.18. For this third case the areas plotted are nested within each other, meaning larger areas include smaller ones. The same author stated that the highest z values are computed across different biota. He cited examples in which the z values ranged from 0.5 to 1.0. Later, Williamson (1981, 1988) found *z* values to span much greater ranges for relationships among real island, habitat islands and mainland samples. It is worth noticing that these different types of species-area relationships are plotted using different methods as in "between islands" and "between biota" examples the sampled areas are not nested while in the "within biota" example the areas plotted are not different patches of the same territory but can be considered as different circles with the same centre but with different diameters. All these values are considered only as a general scheme to distinguish the results coming from different scales of investigation or computed by different methods, even if they provide information about the importance of the heterogeneity of the habitat involved in such a relationship.

The strength of the SAR made it a viable tool in topics as disparate as the estimation of extinction risk in fragmented habitats (Pimm and Askins, 1995; Kinzig and Harte, 2000), latitudinal diversity gradients (Rosenzweig and Sandlin, 1997), paleodiversity (Barnosky et al., 2005) and conservation biology (Myers et al., 2000).

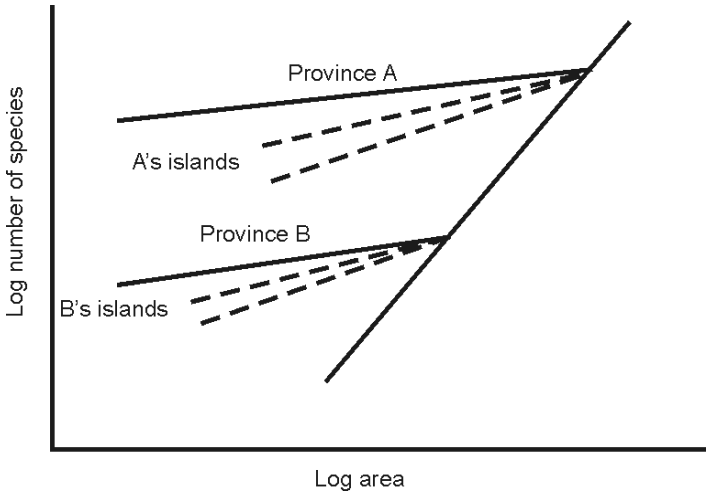


Figure 3.1

3.1.2.1 The hypotheses about the species-area relationship

The most discussed topic about the species-area relationship regards the factors that determine its predictable trend. Two kinds of factors were advocated: the "area *per se*" hypothesis (Preston, 1960; MacArthur & Wilson, 1967; Rosenzweig, 1995; Kallimanis et al., 2008) and the habitat heterogeneity hypothesis (Williams, 1964; Kallimanis et al., 2008). The former typically explains the pattern by considering the increase in the number of the species as a statistical artefact. In other words, it starts from the assumption that species are homogeneously distributed above a territory and that the species included in smaller areas are simply a random sample of the number of the whole territory. According to this, any sampling areas have a probability to detect a number of different taxa that is proportional to their size. Rosenzweig (1995) performed statistical simulations to test if the patterns he found were due to a sampling artefact. He found that the results obtained by the simulations were statistically different from those computed by realistic values of species richness. Gaston and Blackburn (2000) considered such a procedure not to be perfectly adequate to the goal as it is based on some assumptions too strongly dependent on the investigator's choices. They suggested to perform comparisons between all the sampling areas used to drawn the species-area relationships. In this procedure S computed on a small sample (expected data) is compared to the count in another sample but of the same size (simulated data) drawn by larger sampling areas. If each computed expected S is similar to the relative simulated one, then smaller areas are simply random samples of the larger ones,

thereby the pattern is due to sampling artifact. Kallimanis et al., 2008 explained that in case of pattern determined by statistical artifact, at finer scales the species richness increases due to the increase of the sampling intensity, whereas at coarser scales the increase of area determines a similar pattern in population size thus reducing the extinction risk. At this broader scale a new component positively affects the richness by immigration events of new species. Different methods were suggested to test the area "*per se*" hypothesis and in most cases the results demonstrated that this does not explain the observed species-area pattern (Gaston and Blackburn, 2000). This first explanation can have an ecological basis other than a statistical one. Indeed, the Equilibrium Theory of MacArthur and Wilson (1967) provides a valuable contribution to the understanding of such a model (Figure3.2). The Theory affirms that the number of the species actually found on an island is an equilibrium between two opposing forces: the colonization rate and the extinction rate. The former being a flow that increases the number of taxa on an island that decreases when the species pool on the island approaches to the mainland pool. The latter, instead, is a force that tends to decrease the species number and that has its highest intensity in condition of crowding. They demonstrated that the total number of individuals, and so the average population sizes of species, are larger on larger islands. Larger population sizes are likely to reduce the extinction risk, as for their wider variance in character values allows them to overcome strong environmental changes (Gaston and Blackburn, 2000). Then on larger islands the equilibrium between the influences of the two forces is shifted towards higher number of species, whereas on smaller islands this equilibrium only allows a small number of taxa.

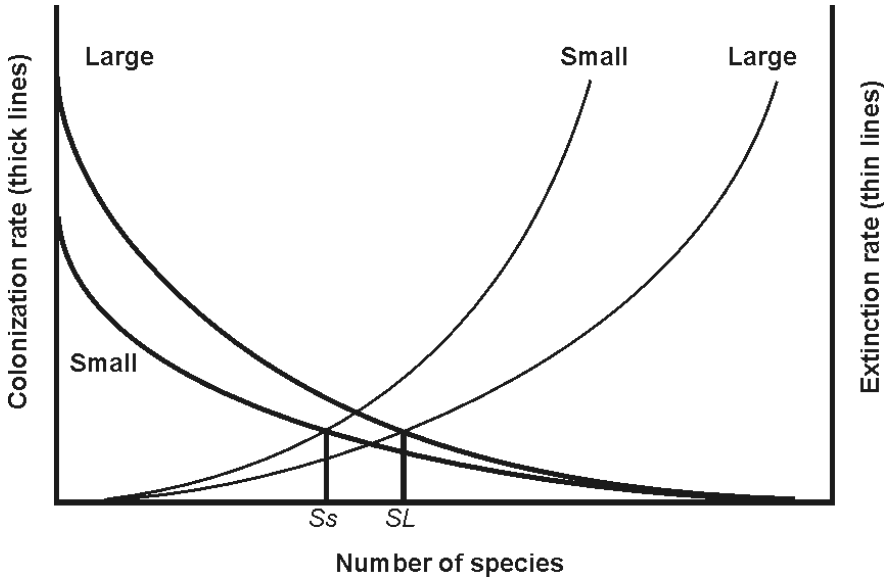


Figure 3.2 Schematic representation of the the Equilibrium Theory of MacArthur and Wilson (1967)

The second most advocated explanation for the species-area relationships is the habitat heterogeneity hypothesis (Williams, 1964). According to this hypothesis larger areas contain more habitats than smaller ones thus leading to a larger number of different species living there. The relationship between area size and number of different habitats encountered was demonstrated in many studies (Hamer and Harper, 1976; Ford, 1987; Kitchener et al., 1980a,b; Reed, 1981; Rigby and Lawton, 1981; Buckley, 1982; Tonn and Magnuson 1982; Fox, 1983; Haila and Jarvinem, 1983; Rafe et al., 1985; Quinn et al., 1987; Rosenzweig, 1995; Sfenthourakis, 1996; Burnett et al., 1998; Kallimanis, 2008). This hypothesis leads to two different predictions (Gaston and Blackburn, 2000): the first is that habitat diversity should be a better predictor of the species richness and the second that if the habitat heterogeneity, considered as a measurable variable, can be maintained constant, then no species-area relationship should be found or the model detected should be equal to the predicted one by "*the area per se*" hypothesis. The first prediction was confirmed by many studies (Johnson, 1975; Reed, 1981, 1983, 1984; Boecklen, 1986; Rafe et al., 1985; Quinn et al., 1987; Peck, 1989;). The number of breading land birds in the on British coastal islands was better predicted by the number of different habitat types than the area measures did (Reed, 1981, 1983, 1984). Kallimanis (2008) went beyond the correlation between the area sizes and habitat

diversity and computed an interaction factor claiming that the covariance between these two variables should be taken into account when performing such analyses. Other studies did not supported the first prediction of the habitat heterogeneity hypothesis (Ford, 1987; McCollin, 1993; Bellamy et al., 1996).

As regards the second prediction a few studies were performed to this aim. The first attempt was made by Rosenzweig (1995) by using the data of birds richness in Bostrom and Nilsson (1983). He showed that area and the avian diversity are unrelated on Swedish peat bogs (considered as examples of constant habitat) once the effect of the sample size was removed (Gaston and Blackburn, 2000). Furthermore Kallimanis et al., 2008, using a model combining the influence of both area size and habitat heterogeneity, including an interaction factor, demonstrated that habitat heterogeneity have a strong influence in increasing species-area slopes as shown in Figure 3.3. Then they performed other statistical analyses to test on one hand the relationship between area and species richness, after maintaining constant the habitat heterogeneity, and, on the other hand, to test the relationship between habitat diversity and species richness but in equivalent sampling size areas. The study showed that in both cases the relationships were always positive and statistically significant, meaning that both area size and habitat heterogeneity have a strong influence on species richness (Figure 3.4).

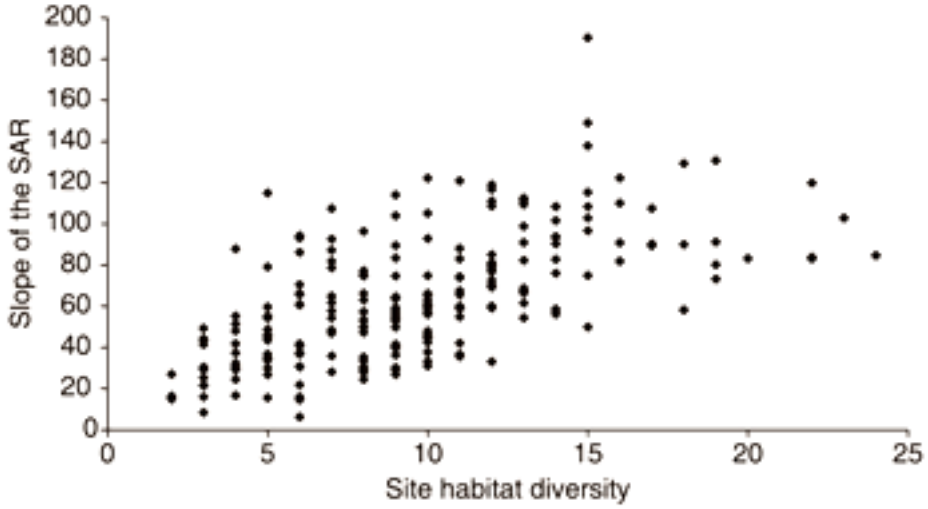


Figure 3.3

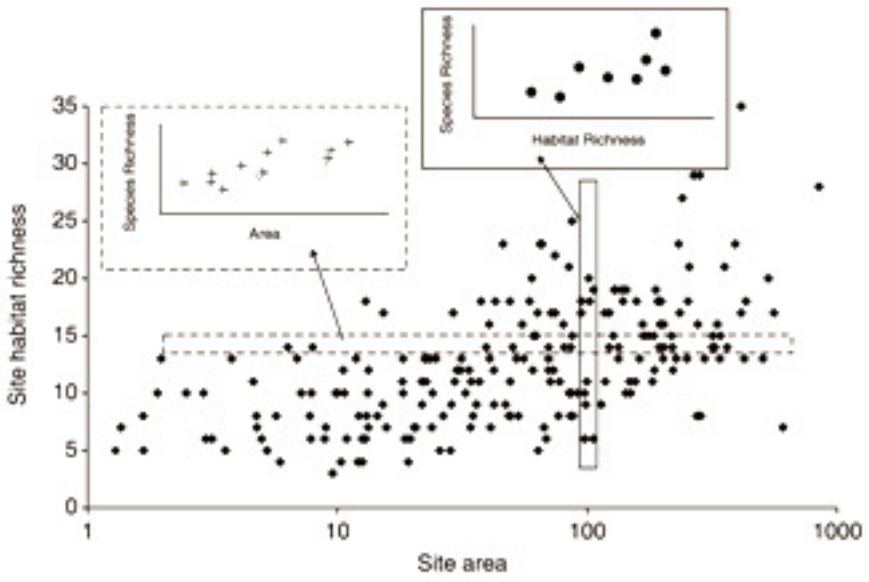


Figure 3.4

3.1.2.2 Combining the "area per se" and habitat heterogeneity influences in the species-area relationship: species-energy and the choros models

The first attempt to combine the effects of the *"area per se"* with ecological factors was made by Wrigth (1983). He improved the island species-area relationship by substituting the island area measures with a new term computed by the product of the area of the islands with a measure of the total energy available in a particular trophic level. Wright (1983) suggested that the species–area relationship was simply the special case of a more general species–energy relationship where resource density does not vary spatially. In his model the ecological term did not estimate directly the variety of resource types present on an island, but was directly correlated with it (Whittaker, 1998). This model was based on the assumption that is the greater the available energy at a site, the more individual organisms (hence species) it can support. He demonstrated the validity of his model providing two empirical demonstrations for angiosperms of 24 islands and for land bird species on a set of 28 islands. As regards the angiosperms, he used as total productivity the measures of evapotranspiration, which represents the amount of water used to meet the environmental energy demand. For bird he used the total net primary production. His models explained the computed variances better than the classical species-area relationship. Wyle and Currie (1993)

applied a similar approach to data on mammals on land-bridge islands and found that island "energy" explained more of the variation in mammal species richness that area alone did. An approach similar to Wright's energy theory is based on the interconnection of the area and habitat diversity. Rosenzweig's (1995) affirmed that area and habitats are so tightly interconnected in nature that can be considered one the surrogate of the other, thus improving the fit to a curvilinear relationship. But if the area is a variable almost simple to measure, the same cannot be said for habitat. Indeed, the habitat concept itself is difficult to define and, thereby habitat, as variable, is very difficult to measure. Newmark (1987) affirmed that the inadequacy of the existing definition of habitat is one of the reasons that prevents the assessment of the relative importance of *"area per se"* and habitat heterogeneity in the species-area relationship. Ricklefs (1979) defined habitat as the vegetative cover of an environment, whereas, according to Whittaker et al. (1972) "habitat is an m-dimensional space in which species exist". This latter definition seems to be the most used in the last decades (Krebs, 1988, 1994; Looijen, 1995, 1998). But the difficult in choosing the m axes made this definition almost fuzzy. Triantis et al. (2003) developed an implemented model of the species-area relationship they called "choros" in which they combined the effect of area and habitat heterogeneity as explicative variables of the species richness. The term "choros" derives from the Greek word that describes the dimensional space. This combined term (K) is simply the product between the area of a region and the number of the different habitats present in that region. Then the choros model takes the form:

$$S = cK^z \qquad 3.3$$

Where k substitutes the term A (area) in the Arrhenius' model. The authors applied the model to the data coming from other studies, performed on islands or mainland, in which the habitats were identified by the vegetational associations. The data used regarded many different taxa such as lizards, mammals, birds, arthropods, vascular and non-vascular plants and amphibians. Once applied, the choros model was compared to the traditional species-area relationship to test the relative goodness of fit. The results showed that the choros model was able to predict the species richness better than the classical one in 20 cases of 22, underpinning the importance of considering the interaction between *"the area per se"* and habitat heterogeneity factors in determining

the number of different species in a region. A general criterion of how to determine the species habitat results as a key topic that will improve the possibility to compare such models between different taxa.

3.1.3 The species-time relationship

Grinnel (1922) was the first to note that more different species were detected when a site was sampled for increasingly long time periods. Later, Williams (1943; 1964) noted a constant increase in sampling new species of insects while doubling the total time of observation. This pattern was also recognized by Preston in 1948, when the proposed that this was the predictable consequence of increasing the sampling efforts. In the 1960 the same author revisited this pattern and recognized it could be statistically formalized in the same way of the species-area relationship, but with the appropriate modifications:

$$S = cT^{w} \qquad 3.4$$

This is the modification of the Arrhenius equation for the species-area relationship (3.1). In the species-time relationship S is the number of different taxa an c is a statistical constant. The new terms T and *w* are the time interval in the sampling operation and the constant rate of taxon increase respectively. A previously mathematical representation was proposed in Fisher et al. (1943), where the logarithmic equation was shown:

$$S = c + wLogT \qquad 3.5$$

The question about the mathematical representation of the specie-time relationship perfectly replicates the one discussed for the species-area fitting model. Some authors found that the power-law model provided the best fit to the used data (McKinney and Frederick, 1999; Hadly and Maurer, 2001). Adler and Lauenroth (2003) showed a quantitative comparison between the power and the logarithmic models by using the relative computed R^2 from Ordinary Least Square for grassland plant. Their results proved that all the data were better described by the power function, but following studies (White, 2004; White et al., 2006), performed on 521 breeding bird communities,

contradicted the previous results highlighting a major role of the logarithmic form, also stating, however, that the difference between the "goodness" of the two models were not statistically significant. Fundamental for this topic were the conclusions provided by Rosenzweig (1995), who stated that it is impossible to find a model that best describes this pattern. A great improvement in the methodological approaches to the STR model was provided by White (2004), who tried to subdivide the pattern in two phases: one characterized by the sampling factors and another mainly determined by ecological ones. As discussed above these results did not solved the node of the best fitting model. Interestingly, He and Legendre (1996) envisaged that, due to the different factors acting at different time scales (see below), STRs performed over evolutionary time periods could be divided in a first phase best described by logarithmic function, in an intermediate time scale phase (during which ecological factors dominate) best described by power-law and in a longer phase spanning over evolutionary times and best described by a logistic curve. At this point it is important to say that although there is a general opinion in considering the equivalence in the goodness of fit of the two described model, the power function is more suited in studies that focus the attention on the species turnover as the exponent *w* is considered as a measure of the relative increase of species richness. For this reason the power-law was used to compare the *w* exponents between different taxa and sampling time interval. When Preston (1960) discussed the properties of the species-time relationship, he stated that STR should be a fairly general pattern with a predictable behaviour at different scales of investigation, as it happens in the case of the SAR. His data on several bird communities confirmed these insights showing the slope values of the logarithmic function of the STRs to be very similar to the equivalent SARs. According to Williamson (1988) and Rosenzweig (1995), the exponents in the power function of STRs are very similar to the SARs' ones when in both sampling areas and temporal time intervals larger samples include smaller ones (nested approach). Indeed, they reported, for both *k* and *w*, values spanning from 0.1 and 0.2. Rosenzweig (1995) also found that STRs computed over fossil data might have higher *w* values than *z* computed on the intra-continental geographic scales, as they are strongly influenced by the contribution of speciation (see below) (Preston, 1960; Rosenzweig, 1998; McKinney and Frederick, 1999; White, 2007). In 2001, Hadly and Maurer showed that for a montane mammal community, in particular sampling conditions, the exponents of the SAR and STR are equal (0.27). More recent studies,

instead, provided contradictory results in which the mean STRs' exponent values can be either similar (White, 2004) or higher (Adler and Lauenroth, 2003) than those of the SARs. Compiling data on all known published studies, power-law STRs provided a tendency for the exponents to average around a value of 0.3, that is very similar to the tendency for SARs' *k* (White, 2007). What seems generally accepted is that the values of the exponents in the power-law for evolutionary time interval should be, as average, higher than those computed in intermediate time spans, whose reasons will be explained in the paragraph dealing with the factors that shape the STR pattern (as explained in the following paragraph).

3.1.3.1 The factors that shape the pattern

In discussing the causes that determine such a pattern, Preston envisaged that three different processes, occurring during three types of temporal scales respectively, can be advocated in shaping the species-time relationship. He named the first process the "sampling error", being conscious that a better definition could be found to express his insights. Indeed, studying the spring migrating avifauna, he affirmed that the newcomers breeding in the state of Pennsylvania, in a particular year, were a random fraction of the regional pool. The following species, arriving later, were forced to migrate elsewhere. Then, he stated that If one would perform a similar study in the following year, the species detected would be different from the preceding one, thus determining an increase in the number of bird species detected in two years. A second kind of "sampling error" can occur (White, 2007). In a static community, the more individuals are sampled the more different species are detected (Fisher et al., 1943; Bunge and Fitzpatrick, 1993; Gotelli and Colwell, 2001) and this happens when the sampling efforts is due to an increased time spent in a survey (Preston, 1960; Rosenzweig, 1995). This statistical artefact occurs because the frequency distribution of a community provides as a results that many species are rare (Brown, 1995; Gaston and Blackburn, 2000), thereby the likelihood to detect them is proportional to both sampling area sizes (see above) and the time spent for the survey. If a site is sampled repeatedly through time the chances of observing a rare species increase as many more individuals are sampled (White, 2007). Preston (1960) talked about a second process occurring during ecological time intervals. Communities change due to the ecological successions and

the succeeding of *seres* determine a temporal turnover in its taxonomical composition. This turnover can be driven by any kind of external factors (volcanic eruption, fire, human impact and so many others) disturbing the habitat as well, thereby breaking the equilibrium of a community and determining a new order in the community assemblage. In other words, during this intermediate temporal scale a particular territory is then characterized by colonization and local extinction events driven by processes that can operate simultaneously with different strength and in synergy. All these phenomena can change the habitat until forcing resident species to migrate towards more suitable habitats and providing a favourable new ground for newcomers. The third temporal scale regards the processes involved during geological time scales and that lead to the evolutionary changes in species composition of regional biota. Preston, referring to fossil records, talked about a correspondence with Wetmore, who explained that few of the actual bird species had their relative fossil occurrences since the late Pliocene, establishing as distinct entities at the beginning of the Pleistocene. According to Brodkorb (1958) all the bird genera of the Middle Pliocene occur in the present avifauna of Oregon, whereas the relative species are all extinct. This means that the number of genera remained substantially invariant while there was a strong turnover in species. This is what happens when considering evolutionary times of observation, during which speciation and extinction events begin to dominate the cumulative increase in species richness (Preston, 1960; Rosenzweig, 1995; White, 2007).

3.1.4 STAR model: combining the effects of both area and time in species accumulation

As said above, Preston (1960) proposed that the species-time relationship should behave in the same way that the species-area relationship does. This advocated equivalence, expressed in his famous conjectures, was shown by the author explaining that the species accumulation in time should vary with spatial scale of observation. Thereby, repeated samplings in a plot of a certain size would have produce an STR with a scaling exponent equal to that of the SAR. Later, Rosenzweig (1998) realized that both sampling area sizes and sampling time interval affected the species richness.

Indeed, in the attempt to draw a species-time relationship with fossil data, he noted that different periods of time in fossil records were associated with different areas of rocks containing the fossils to be sampled. In this study Rosenzweig proposed to control for this effect the use of two new models. The following equation represents the first model proposed by Rosenzweig and that he called the "no interaction model":

$$S = cA^{z}T^{w} \qquad 3.6$$

In which he combined, by multiplying, both the effects of the SAR and STR, that, in this equation, assumes they operate independently from one another. Then he build a second model in which a new constant was added to the equation 3.6 that described the time dependence. While the described assumption of independence effects of time and area on species accumulation could appear reasonable, the models provided by Rosenzweig were to simple to describe a species-time-area relationship (STAR) (White, 2007). Adler and Lauenroth (2003) and Adler et al. (2005) provided a more complex model (the "Full model") to describe the influences that both area and sampling time interval could exert on the species accumulation. Moreover they introduced an interaction factor that explained the variation of the species richness in the sampling areas by considering increasing sampling time interval and vice versa. The equation of this model was formalized by:

$$S = cA^{(z1 + [u/2]\log T)}T^{(w1 + [u/2]\log A)} \qquad 3.7$$

The new terms in this equation are z_1, w_1 and u. The first two terms represents the scaling exponents of SAR and STR at unit spatial ($1m^2$) and temporal (1 year) scales respectively. The term u is the already described interaction factor. After computing u, the equation 3.7 allows to compare the spatial and the temporal species turnover, as explained below. In the 2003 Adler and Lauenroth used this equation to study the richness in grassland communities in Kansas (Hays and the Konza prairie) using data coming from long term surveys (35 years for Hays and 20 years for Konza). The sampling areas were quadrants of 1 m^2, whereas the sampling time intervals were constituted by equals "temporal windows", that is to say each quadrant was monitored year per year, thus providing as many temporal windows as are the total years of the

survey. The increase of the sampling area size was obtained by summing the different quadrants, whereas the time intervals were increased by summing succeeding temporal windows. The aims of this study were not only to draw SARs and STRs alone, but to compute the value of the interaction factor that describes, as said above, how the increase of spatial samples could affect the STRs' exponents and vice versa. The results provided by the authors showed that, for the data considered, the STRs' slopes were higher than the SAR ones. The more important result was that the interaction factor u has negative values indicating that space and time interval influence each other negatively. In details, this means that when performing STR models, considering the same time intervals, but on succeeding increased sampled areas the w values tend to decrease (Figure. 3.5a-c). The same variation was obtained when maintaining constant the number of quadrants and varying the sampling time interval (Figure. 3.5b-d).

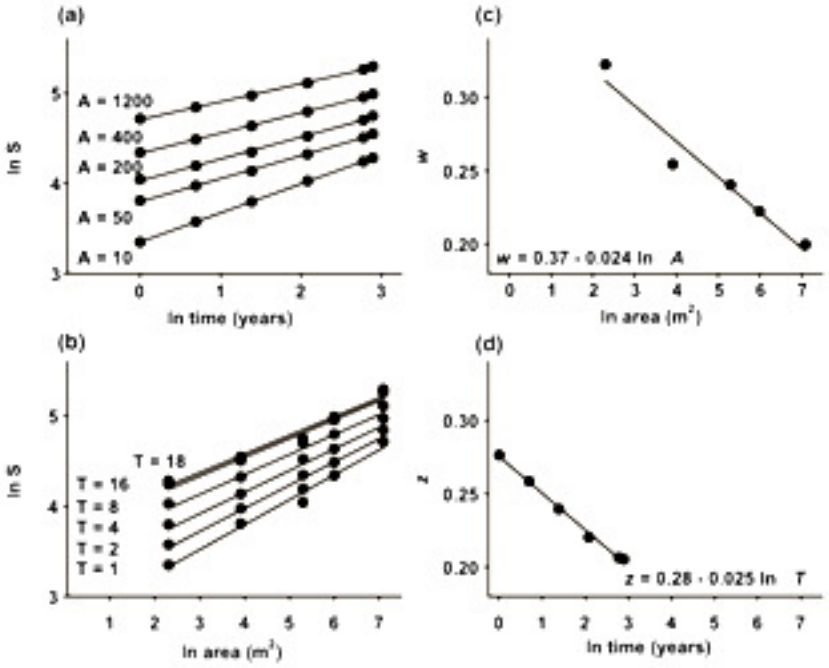


Figure 3.5

Later, Alder et al. (2005) showed a study in which they tested what model better fitted with their data between the Adler and Lauenroth (2003) "Full model" and the "no interaction model" and the "simplest model" provided by Rosenzweig (1998). They also highlighted the importance to use the interaction factor to compare the spatial and temporal turnover of species. Indeed, as demonstrated in Adler and Lauenroth (2003), if

the “full model” best describes the data, then interaction term complicates this comparison as it means that temporal turnover would change as a function of the spatial scale. In these case, the only way to do such a comparison is to use what the authors called “scales of time-area equivalence”. Using these scales it is possible to obtain particular combinations of sampled area and time interval by which the measured rates of spatial and temporal turnovers are equals. The scales of equivalence can be obtained by the equation:

$$A/T = 10^{[(z1-w1)/u]} \qquad 3.8$$

obtained by the 3.7 and substitute the computed values of *u*, *z1* and *w1*.
To these aims they used eight assemblages of different taxa (spanning from intertidal algae to grassland prairies, from lake zooplankton to desert small mammals), some of these displaying long term data. The authors demonstrated that in every case the “Full model” best described the data. All the computed interaction terms were negative and were used to compare the spatial and temporal species turnover. In general these studies provided the proof of the existence of a species-time-area-relationship (STAR), a pattern that cannot be determined by the sampling effect alone, but by the spatial and temporal heterogeneity of habitat (White, 2007).

3.2 Material and Methods

3.2.1 Setting the data for the analyses

Using the incidence matrix presented in the chapter 1, the recorded localities were used to compute both SAR and STR models, plus the “Full model” provided in Adler and Lauenroth (2003). The ages of the localities used were those computed by the regression equation between the geochronological ages and the mean age estimates based on Fiedler and MA AEO scores, as explained in Chapter 2. In order to perform the described analyses, the total of 781 localities, along with their geographical

coordinates, were imported in ESRI ArcGis 9.2 to create a point shapefile describing the geographical distribution of all LFAs. As one of the aims of this project was to compute geographical areas, it was useful to project the data frame into the Lambert Azimuthal Equal Area projection. This was necessary as, considering a large territory, non projected data are characterized by the distortion that occurs along the meridians, due the variation of world's curvature radius along meridians Then, via the "Point to Raster" tool of the same software an equal area cell grid was built, whose geographical extension was determined by the distribution of the localities itself. As for the low density in the geographical distribution of fossil localities, the cells in the grid had a very large geographical coverage estimated in 500,000 Km^2. The creation of such an equal area cells grid was necessary to avoid to sample at different geographic scales and to reduce the area effect on the STR calculation. Using the library "Hawk tools", the computation of the number of localities in each cell was performed. For the analyses only cells with 7 localities at least and with a time span equals or larger than 2 million of years were considered. Finally 12 cells were recognized to satisfy all the described conditions and are those provided of and identification-number in Figure 3.6).

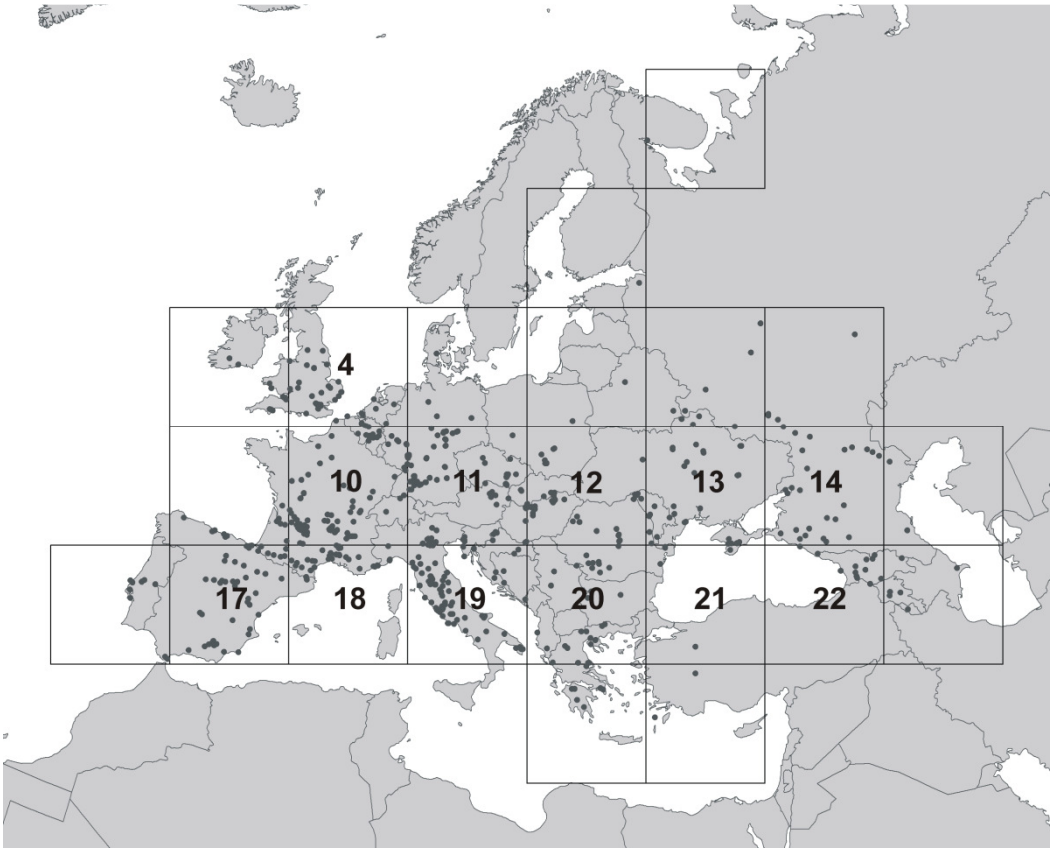


Figure 3.6 Geographical grid built for the computation of the statistical models

3.2.2 STR calculation and the application of the correction factors

As the aims of this research did not focus on the determination of the best fitting model but on the estimation of the temporal and spatial turnover, only the power-law equation provided by Arrhenius (1921) was used for both STRs and SARs.

For each cell, cumulative abundance of different species, *S,* was computed by partially automatic operations in Microsoft Excel, by chronologically ordering the localities and considering their faunal lists. Then, locality after locality the accumulation of new species was computed. As regards the fossil records, in each cell there were some temporal gaps that could affect the computation of the specie richness. Indeed, it was not possible to detect the species that probably lived exclusively during these gaps. Kinzing and Harte (2000) proposed a mathematical equation to estimate the number of endemic species included in known geographical portions of lost habitat (phenomenon due, for example, by human activity or natural disaster). As these species are considered endemic of the lost portions of territory, they could not be detected in a survey. The estimation of the number of these species is given by the following equation:

$$E(A) = (A/A_0)^{z1} S_0 \qquad 3.9$$

Where E is the number of endemic species lost with the A_o portion of the total area A, S_0 is the species richness computed in A and z1 is the new spatial scaling exponent computed applying the formula:

$$z^1 = -\ln(1-1/2^z)/\ln 2 \qquad 3.10$$

This equation was modified to the aims of this research and thereby converted to the estimation of endemic species lost in temporal gaps. Then, the term A was substituted by T (the total time interval determined by the estimated ages of the oldest and youngest localities) and T^0 (the duration of the temporal gap), whereas z and z^1 were replaced by w and w^1. S0 is the number of different species computed in the total time interval covered by the localities of a particular cell. The new equation is:

$$E(S) = (S/S_0)^{z1} S_0 \qquad 3.11$$

Temporal gaps in a cell was considered as any time intervals between two following localities that was larger than the 20% of the total cell time span. The number *E* of endemic species in a particular cell was summed to the relative value of S (computed before the correction). As result, for each cell, a new value of species accumulation, defined S_e, was obtained and used to compute all the STRs models. Furthermore, another kind of correction was performed, but separately from the previous one, to correct for the different sampling biases that characterize the fossil records considered, this latter covering a very long time interval (more than 3 Mya). Indeed, it is known that the fossil localities record is uneven distributed in the considered time interval, with fewer localities occurring in older periods, as discussed in the first chapter. Then, a statistical technique called rarefaction analysis (Gotelli and Collwell, 2001) was used that allows to estimate the number of items (mammal species, in this specific case) when using different sampling efforts (uneven distribution of localities along the considered time interval). The analysis uses the number of species occurrences in the cell with the greatest number of localities to estimate S_r (rarefied estimate of *S*) in the other locality-poorer cells. The values of S_r were, then, compared to the *S* and S_e. Finally an STR was computed considering the total temporal range size of 3.7 Mya and all the previously described procedures to estimate S_e were then applied for the computation of this STR. In this case all the 781 localities were collated by their age estimates and the computation of *S* was performed locality after locality, as done for each singular cell. The use of the total sample of LFAs drastically reduced the frequency of temporal gaps, thereby fewer corrections were needed.

3.2.3 Comparing slopes at different time periods

STR slope was investigated to test if it increased in the last million years, that is since climate switched to the most intense oscillations. To this aim the record was divided into 1 May long intervals, and different slopes were calculated at the 3-2, 2-1, and 1-0 Ma intervals. As the first (3-2) interval includes the lowest number of localities (22), this time bin was considered as a reference estimate. Thereby, twenty-two localities were extracted at random from each of the two succeeding (2-1; 1-0) time intervals. Then the STR slopes were computed. This algorithm was repeated 1000 times for each time-

interval in order to generate a family of slopes to be compared with each other and with the reference estimate. In addition, for each randomly-generated sample, the total number of occurrences was recorded, whereas samples having more than 110% and less than 90% of total occurrences than the reference sample (i.e. that of the 3-2 Ma interval) were excluded. This criterion was applied to prevent comparing slope values flawed by total occupancy, which alters diversity count consistently. No random sample having a duration less than 900 Kya was included.

Finally, the computation of instantaneous slopes between any two successive localities with different ages and non-zero increase in diversity was performed and graphically represented.

3.2.4 The computation of the SAR

As the temporal issue discussed above did not affect the computation of the SARs, only the original values of the species richness (*S*) of each cell were considered to compute the species-area relationship. The increase in sampling size was obtained by creating groups of 2, 4, 8 and 12 cells. As for these groups many combinations of different cells can be obtained (there are 12 possible combinations of group size = 1 cell, 66 of group size = 2 cells, 495 of group size = 4 cells and so on), each cell was assigned an identification-number (the number of the cells in Figure 1) and, then, there was the computation via R software of all the possible identification-number combinations. The *S* value for each group was obtained by computing the arithmetical mean of the species richness obtained for all the possible combinations. As many cells included sea portions, the area of a cell constituted by sea surface was erased and only the areas of land territories were considered in the analyses. This operation was performed in ESRI ArcGis 9.2 by subtracting a shapefile of the sea surface from each cell-grid shapefile. Then the cells' areas were expressed by fractions of the unitary value (i.e. 500,000 Km^2). As for the STR, a rarefied model was built for the species-area relationship, by considering the most localities-inclusive cell as reference value.

3.2.5 The STAR model

For the computation of the STAR model it was necessary to built a matrix of *S* values for all possible combinations of spatial and temporal sampling sizes. To this aim discrete sampling temporal increases were considered: from 3.7 to 3.0 Mya, from 3.0 to 2.0 Mya, from 2.0 to 1.0 Mya, from 1.0 to 0.5 Mya, from 0.5 to 0.1 Mya and from 0.1 to 0.01 Mya. Then, for all the possible combinations of 2, 4, 8, and 12 cells there was the computation of the *S* values at each of the established temporal sampling sizes. As different S values were available for each spatial sampling size combination at a determined temporal sampling bin, the arithmetical means ware considered as entry data for compiling the matrix. All these data were then fitted to the Full model used in Adler and Lauenroth (2003) and in Adler et al., 2005 in the logarithmic form:

$$\log S = \log c + z_1 \log A + w_1 \log T + u(\log A)(\log T) \quad 3.12$$

A second STAR computation was then calculated adding a fifth term (the logarithm of the total number of LFAs at given space and time parameters), to correct for the number of sites contributing to a given S value (we had noted the number of sites per cell significantly affects S at the level of cells; n = 12, r = 0.798; p = 0.002). This second STAR model takes the form:

$$\log S = \log c + z_1 \log A + w_1 \log T + u(\log A)(\log T) + b\log\mathrm{LFAs} \quad 3.13$$

The ability of both STAR models to predict S at various combinations of time and area was assessed calculating deviations (sum of squared deviations) from real data, and by applying a chi-2 test. Both STAR models were applied to both raw data, and the ones corrected for “time endemics”. Although any estimation of STAR predictive power of diversity is senseless in the latter cases, their exponents w, z and u could be compared with STAR computed with raw data for comparison as for a further insight on the influence of sampling bias.

3.3 Results

3.3.1 The SAR and the STR

Cell diversity S_0 varies in between 36 and 102 species (mean = 73.1) (see Table 3.1). Uncorrected STR slope *w* varies in between 0.482 and 2.907 (R^2 range 0.645-0.944) with fitting based on power functions. S_e varies in between 53 and 180 species (mean = 105.2). Slopes with the correction for "time endemics" varies in between 0.542 and 1.016 (R^2 range 0.806 – 0.986). The variance in *w* with correction for time endemics is 33 times lower and R^2 is, on average, 6% better than with raw values (Table 3.2, Wilcoxon W = 61, p = 0.012, one tie removed). In addition, average diversity S_e is close to maximum raw diversity (105.2 versus 102). These results indicate that the correction for "time endemics" was successful. Rarefied diversity estimates S_r are very close to true S (chi-2 test: p = 0.130) meaning that differences in *S* among cells almost entirely depends on sampling biases.

Total-sample STR slope is higher than with single cells, $S(T) = 5.87E\text{-}007\ T^{1.290}$ (F = 20834.4, n = 439, $R^2 = 0.979$, $p < 0.001$, see Figure 3.7). STR corrected for sampling inequality describes a shallower curve ($S(T) = 5.87E\text{-}007\ T^{1.090}$, n = 149, $R^2 = 0.971$, $p < 0.001$, see Figure 3.7). Total-sample SAR takes the form $S(A) = 70.53A^{0.416}$ (F = 126.7, n =12, $R^2 = 0.927$, $p < 0.001$, see Figure 3.8). SAR corrected with rarefaction offers a slightly better fit and lower scaling exponent $S(A) = 1.592A^{0.274}$ (F = 135.9, n =12, $R^2 = 0.931$, $p < 0.001$).

3.3.2 Slopes per time

The single STR for the 3-2 Ma interval gave a slope of 0.67 ($R^2 = 0.593$). The average slope over the 2-1 Ma interval is 0.188 (range 0.03 – 1.12, mean $R^2 = 0.703$), while average slope over the 1-0 Ma interval is 0.367 (range 0.06 – 0.68, mean $R^2 = 0.666$; Table 2). These results indicate slopes are sensitive to total time span (becoming lower over shorter intervals) and to time gaps, as range is much higher in the poorer sampled

2-1 Ma interval (Figure 3.9). Eventually, there is statistically significant indication that slopes are twice as high at the 1-0 Ma interval ($p < 0.01$).

3.3.3 STAR models

In all STAR models we calculated the z_1 exponent is well in the range of published SAR slopes for curves sampled across different bioprovinces. The STR scaling exponent w_1 is close to the upper limit (1.2) reported by Rosenzweig (1998) for STRs calculated over evolutionary time. The corrections for the number of sites recorded at the various combinations of time and space reduce consistently both slopes, and the correction for time endemics decrease them even further.

Sample size-corrected STAR's sum of squared deviation (2119.1) is lower than the uncorrected model sum of squares (2542.0) and provides a better fit ($chi\text{-}2_{corrected\ STAR}$, $p = 0.47$; $chi\text{-}2_{uncorrected\ STAR}$, $p = 0.20$) (this confrontation was not done on data corrected for time endemics). In fact, the "corrected" STAR provides better estimates for 20/30 (67%) observations, and this is a statistically significant difference (binomial distribution, $p = 0.028$).

Not surprisingly, STAR models are not good predictors of cell diversity S_0, that is at unit spatial scale, that we know from rarefaction analysis it is heavily influenced by total occurrence ($STAR_{non\text{-}corrected}$ $r = 0.392$, $p = 0.207$; $STAR_{corrected}$ $r = 0.112$, $p = 0.718$). As the spatial scale increases, and gaps decrease in importance to vanish altogether, STAR models, and especially the one corrected for sample size, perform better and better.

The interaction term u is negative in all STARs, giving robust evidence that STR slope decreases as the spatial scale increases and vice versa. The regression of SAR slopes on time is significant, $b = -0.254$; $R^2 = 0.78$; $p = 0.018$. The same goes on regressing STR slopes on space, $b = -0.218$; $R^2 = 0.868$; $p = 0.021$ (Figure 3.10).

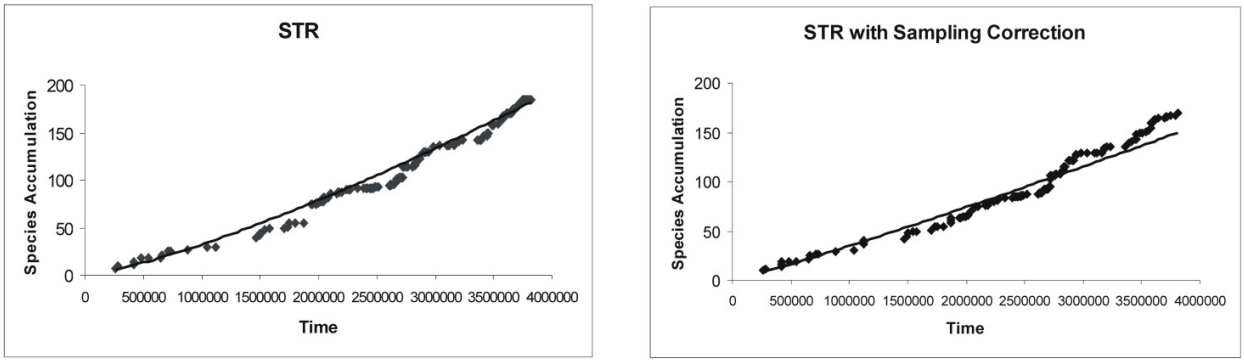


Figure 3.7 STR computation (on the left) and STR with sampling correction (on the right)

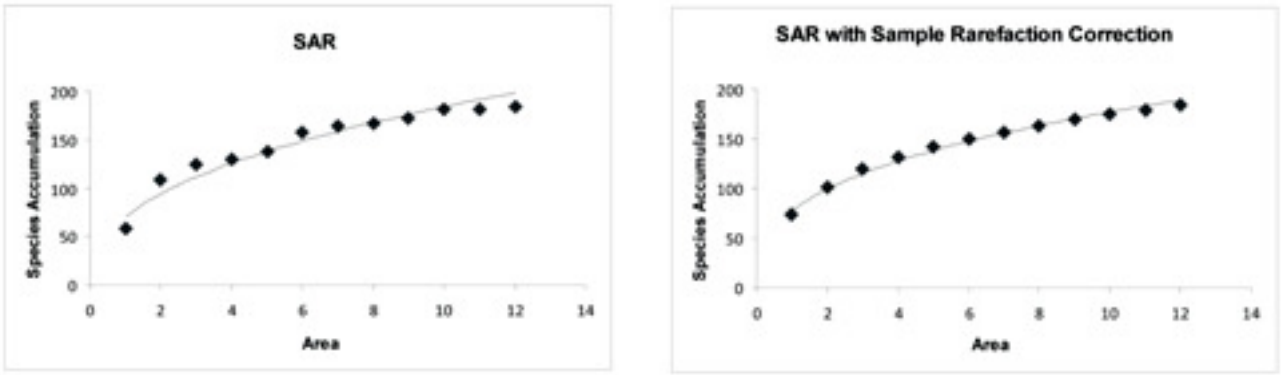


Figure 3.8 SAR computation (on the left) and SAR with rarefaction correction (on the right)

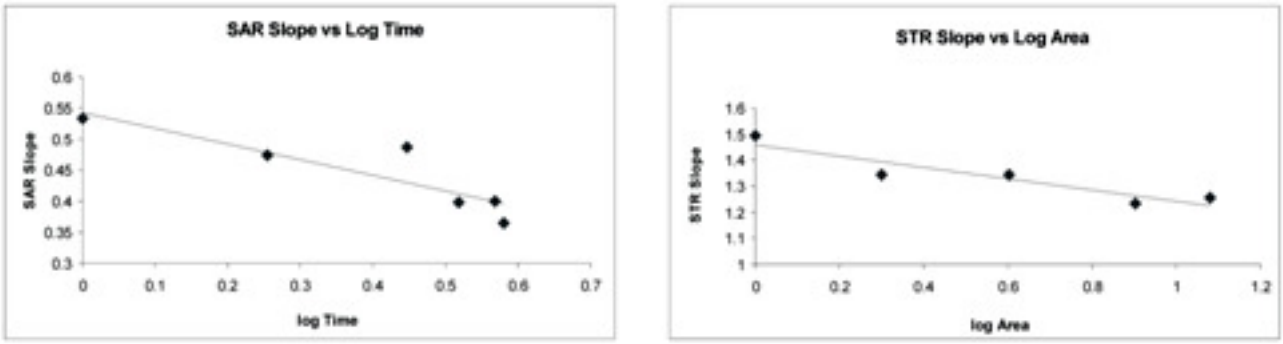


Figure 3.9

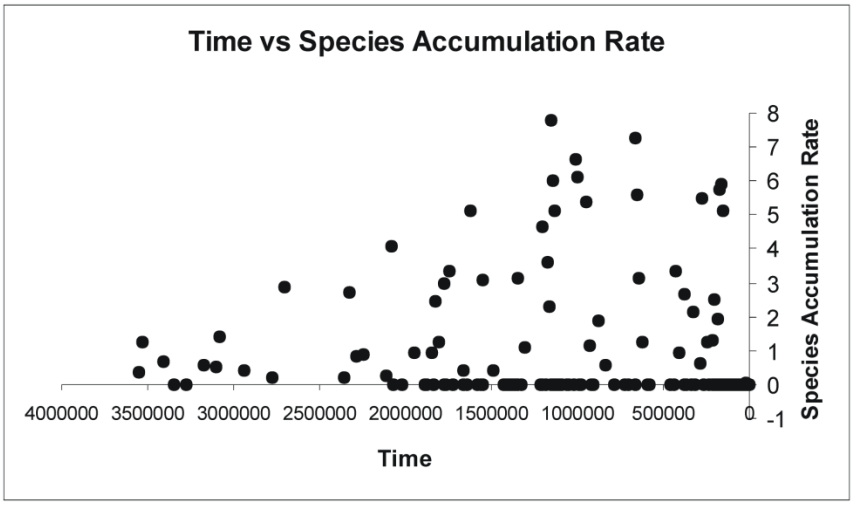


Figure 3.10

Table 3.1 – Cell LFA richness, total species occurrences, diversity counts, time span of included LFAs, and STR slopes (*w*).

cell #	duration (Ma)	# occurrences	# LFAs	*Sr*	S_0	S_e
4	1.862	352	45	71.2	58	76
10	2.682	1260	139	102.8	102	118
11	2.935	1251	134	102.6	99	180
12	3.544	385	48	73.5	60	71
13	3.395	260	32	63.4	56	79
14	3.401	244	30	61.7	78	134
17	2.313	456	52	77.9	96	91
18	3.150	364	37	72.1	73	149
19	3.809	764	88	90.9	90	125
20	2.685	311	36	68.0	81	121
21	3.049	66	7	33.1	36	53
22	1.775	132	15	47.1	48	65

Table 3.2 – slopes and squared R coefficient for STRs calculated over single cells, without (raw values) and with correction for time-endemics (noted with the *e* subscript)

cell #	$w_{raw\ values}$	$R^2_{raw\ values}$	w_e	R^2_e
4	0.593	0.860	0.710	0.930
10	0.897	0.851	1.023	0.894
11	1.966	0.872	0.736	0.821
12	0.482	0.789	0.542	0.841
13	0.725	0.870	0.914	0.941
14	1.386	0.791	0.662	0.902
17	0.828	0.942	0.828	0.942
18	2.907	0.900	0.740	0.906
19	0.909	0.645	0.825	0.919
20	1.176	0.944	0.795	0.965
21	0.526	0.905	0.759	0.938
22	0.653	0.916	0.869	0.986

3.4 Discussion

3.4.1 The STR and SAR models

In STR model performed with the whole sampling data of 781 localities the slope has a value higher than the range recorded for actual species (0.2-0.4 in Connor and McCoy, 1979). This result is in agreement with the second Preston's conjecture, according to which models built over very large time intervals show steeper curves (Preston, 1960; Rosenzweig, 1998; McKinney and Frederick, 1999; Adler and Lauenroth, 2003). This was due to the fact that, during the temporal interval considered in this research (3.8 May), the speciation events strongly contributed to the increase in species' number, while models built with data sampled at the ecological temporal scale rarely account for such evolutionary events. Furthermore, by a visual inspection of the computed STR, the model shows many consecutive steps instead of a straight line. This "staircase shape" is not determined by paucity of fossil record as it occurs during both oldest and in youngest time intervals, the latter containing the largest number of localities. Probably this particular shape represents the effects of the climatic changes on the mammal community assemblages. Indeed, the height of each step could represent periods of deep taxonomical turnover due to stressed climatic conditions, followed by periods during which ecological interaction dominated. STR's slopes are considered to be a indirect measures of the temporal turnover rates (Rosenzweig, 1998; White, 2004), The performed tests for the estimation of slopes in different time periods of the Plio-Holocene showed that there was a net increase in turnover rates in the last 1.0 Mya, as Meloro et al., 2008 already pointed out.

As regards the SAR model, its slope is very close to the higher extreme range (0.1-0.3) found for models built on actual species, as reported by Connor and McCoy (Connor and McCoy, 1979) for intra-continental data range. "*The Initial Step Rise*" (Preston, 1960) that it is possible to observe in the Figure 3.8 is due to the fact that there is a too low species count of species for the one cell sampling size, Although results confirms that the SAR with the sample rarefaction correction is very similar to the model built over the raw data, in the corrected model the "step" visibly reduced, suggesting that the sampling corrections were concentrated at the smaller spatial sampling size.

3.4.2 The STAR model

The computation of the interaction factor (*u*) provided negative values both for corrected and uncorrected STAR models, a result that is in agreement with living species data (Adler and Lauenroth, 2003, Adler et al., 2005). This fact confirms the Preston's second hypothesis (Preston, 1960, but attributed to Rosenzweig, 1998 by White, 2007) about the negative relationship between the species accumulation over time and space. This implies that, as already said, the number of species over time intervals decreases when considering increasing spatial sampling sizes and *vice-versa.* In this view SAR and STR become two different dimensions of the same model which goes under the name of STAR (Adler and Lauenroth, 2003, Adler et al., 2005). The species-time-area relationship, is a much more complex model and draws a more realistic picture of what happened during the last 3.8 May in the Western Eurasia. Indeed, one ready results of the STAR is the time-area equivalence scale (Adler et al., 2005) which explains the relative weight of the time and area's turnover rates. This scale factor shows that the species accumulation over time intervals was faster than the one with the increasing of area sampled, that is to say time's turnovers had a more important role on the species accumulation than area' s. This fact perfectly agrees with the difference between the slope value of the STR and the SAR.

3.4.3 The models under the light of the paleobiogeographic events

The SAR slope value is surprisingly too small compared to the STR' s one. The SAR scaling exponent is generally attributed to the heterogeneity of the habitats embraced as the sampled area increases, thus determining a spatial turnover of species (Rosenzweig, 1995; 1998; Gaston and Blackburn, 2000; White, 2007; Kallimanis et al. 2008). During the period that spans since the Pliocene to the Early Holocene, global climate changes, due to Milankovich cycles, strongly affected the distribution of habitat on the Earth (Lister, 2004). This determined a turnover of species in both the spatial and temporal dimensions. In details, these climate changes, occurred during geological time scale, extremely and repeatedly influenced the ecosystems of the higher and middle latitudes. Mammalian communities responded to these changes with new assemblages

as new species or immigrant ones filled niches become empty for migration or extinction events. That is to say, the ecosystems overcame these changes by their resilience ability in the continuous aim to maintain their stability, consisting in a rearrangement of species and their ecological function (Peterson, 1998). According to the Vrba's "turnover pulse" hypothesis, in some cases, the turnover was due to dispersal events of mammals that migrated towards their preferred habitats for the expansion or regression of ice plates, that is to say when climate became cooler or warmer (Vrba's "traffic light" and "relay" models, Vrba, 1995a, b). In other cases, the extreme climate changes drove to the extinction of some species or to speciation events, contributing to the increased species accumulation registered over time, this determining the recorded very high slope of the STR curve.

As a consequence of the changing temperatures caused by Milankovitch Cycles, the same latitudinal ranges displayed different kinds of ecosystems during different moment of the considered temporal interval. In many cases some species, adapted to particular temperature ranges, migrated and dispersed to find more suitable habitats elsewhere. In other cases, other species overcome adverse climatic conditions by using different refugia (Sommer and Zachos, 2009). In this way these species were pre-adapted when favourable climate conditions occurred (Lister, 2004) In particular, the persistence of these species is probably responsible to the relative low scaling exponent of the SAR as they were able to migrate and colonize different latitudinal ranges that, in different time periods, were characterized by the same habitats. This fact probably decreased the number of new species that could be counted when sampling fossiliferous localities distributed above very large geographical surfaces (such as the one analyzed in this research) and spanning in time over period as long as to embrace mode that one climate cycles.

4 - The General Conclusions

Statistical analyses always applied to living species can be performed to detect macroecological patterns in the fossil faunas too. As demonstrated by Kidwell and Flessa (1996), fossil mammals can be used in macroecological investigations as for their high preservation potential. The amount of fossil data grows up when the time interval of interest is not too far in the past. The same can be said for data reconstructing the paleoclimate, as accuracy of the data reasonably decreases with the temporal scale. For these reasons, this doctoral thesis focused on the mammal faunas that lived in the last 3.8 Mya and because, douring the Quaternary, the well known climatic changes influenced faunal evolution, providing a paleontological prespective of past communities' assembly. From this point of view, the detection of the EA PCOMs represents the ground for performing very long term studies, as done for reconstructing occupancy trajectory and species-time and species-area relationships. Moreover, the drowing of the occupancy course rises some remarks about the condition of a species when it is close to the extinction, as pointed out by Foote (2007).

The spatial scale provided (the Western Eurasia) is large enough to detect mammal dispersals, thus highlighting the attempts of faunas to overcome strong environmental changes by their "long jurneys" towards the suitability. The results of this doctoral thesis show that, by the use of statistical techniques, fossil mammal faunas can provide interesting insights about the composition of past communities, going over the limitations imposed to the biocrhons about the geographical boundaries of faunal assemblages.

The rise of information about phylogenetic relationships between extant and extinct taxa made it possible to know if some characteristics at species and genera levels are hereditable or not and if there are some relationships between them. The taxa analized showed that, in addition to a biological traits, such as the body mass, tipically ecological traits (some measure of occupancy and range size) can be hereditable as well, providing further insights for the controverted topic of the species selection.

APPENDIX A - SYNONYMS AND MOST COMMON SCIENTIFIC NAMES OF THE SPECIES INCLUDED IN THE DATABASE

Most used scientific names	Synonyms
Aceratherium incisivum	*Aceratherium incisivum*
Acinonyx pardinensis	*Acinonyx pardinensis*
Aepyceros melampus	*Aepyceros melampus*
Agriotherium insigne	*Agriotherium insigne*
Agriotherium intermedium	*Agriotherium intermedium*
Alces alces	*Alces alces*
Alephiris lyryx	*Alephiris lyryx*
Alephis boodon	*Parabos boodon*
Alopex lagopus	*Vulpes lagopus*
Anancus alexeevae	*Anancus alexeevae*
Anancus arvernensis	*Mastodon arvernensis*
Antilope koufosi	*Parastrepsiceros koufosi*
Antilospira gracilis	*Antilospira gracilis*
Antilospira zdanskyi	*Antilospira zdanskyi*
Arvernoceros ardei	*Arvernoceros ardei*
Arvernoceros verestshagini	*Arvernoceros verestshagini*
Axis farnetensis	*Pseudodama eurygonos*
	Pseudodama nestii eurygonos
	Axis eurygonos
Axis flerovi	*Axis flerovi*
Axis lyra	*Pseudodama lyra*
Axis nestii	*Cervus nestii*
	Dama nestii vallonetensis
	Dama vallonetensis
	Pseudodama nestii
Axis shansius	*Axis shansius*
Bison menneri	*Bison menneri*
Bison priscus	*Bison priscus*
Bison schoetensacki	*Bison schoetensacki lagenocornis*
	Bison schoetensacki voigtstedtensis
Bos primigenius	*Bos primigenius*
Bubalus murrensis	*Bubalus murrensis*
Camelus knoblochi	*Camelus knoblochi*
Canis adoxus	*Eucyon adoxus*
Canis apolloniensis	*Canis arnensis*
	Canis aff.arnensis/mosbachensis
Canis etruscus	*Canis etruscus*
Canis kronstadtensis	*Canis kuruksaensis*
Canis lupus	*Canis lupus mosbachensis*
	Canis major
	Canis spelaeus
Canis michauxi	*Canis michauxi*
Canis mosbachensis	*Canis mosbachensis*
Canis neschersensis	*Canis neschersensis*
Canis senezensis	*Canis senezensis*
Canis tengisii	*Canis tengisii*
Capra caucasica	*Capra caucasica*
Capra ibex	*Capra ibex-pyrenaica*

Capra pyrenaica	*Capra pyrenaica*
Capreolus australis	*Capreolus australis*
Capreolus capreolus	*Capreolus major*
Capreolus constantini	*Capreolus constantini*
Capreolus pygargus	*Capreolus pygargus*
Capreolus suessenbornensis	*Capreolus capreolus suessenbornensis*
	Capreolus sussenbornensis
Ceratotherium praecox	*Ceratotherium praecox*
Cervalces carnotorum	*Alces carnotorum*
Cervalces gallicus	*Alces gallicus*
	Libralces gallicus
Cervalces latifrons	*Alces latifrons*
	Praealces latifrons
Cervavitus variabilis	*Cervavitus variabilis*
Cervodama pontoborealis	*Cervodama pontoborealis*
Cervus ardei	*Cervus ardei*
Cervus australis	*Cervus australis*
Cervus elaphus	*Cervus acoronatus*
	Cervus elaphoides
	Cervus reichenaui
	Cervus simplicidens
Cervus peloponnesiacus	*Cervus peloponnesiacus*
Cervus perrieri	*Cervus warthae*
Chasmaportetes lunensis	*Chasmaporthetes lunensis*
	Chasmaportetes kani
	Euryboas lunensis
	Lycyaena lunensis
Coelodonta antiquitatis	*Coelodonta antiquitatis*
Crocuta crocuta	*Crocuta crocuta praespelaea*
	Crocuta crocuta spelaea
	Crocuta spelaea
	Hyaena spelaea
Croizetoceros ramosus	*Anoglochis ramosus*
	Cervus pyrenaicus
	Cervus ramosus
	Croizetoceros pyrenaicus
	Croizetoceros senezensis vireti
	Croizetocerus ramosus gerakarensis
	Croizetocerus ramosus medius
	Croizetocerus ramosus minor
	Croizetocerus ramosus ramosus
Cuon alpinus	*Cuon alpinus*
Cuon priscus	*Cuon dubius stehlini*
	Cuon stehlini
Dama clactoniana	*Dama dama clactoniana*
Dama dama	*Cervus cornaliai*
	Cervus somonensis
	Dama somonensis
Damalops palaeindicus	*Damalops palaeindicus*
Deinotherium giganteum	*Deinotherium giganteum*
Dihoplus schleiermacheri	*Dihoplus schleiermacheri*
Dinofelis diastemata	*Dinofelis diastemata*
Dmanisibos georgicus	*Dmanisibos georgicus*

Elaphurus eleonorae	*Elaphurus eleonorae*
Elasmotherium caucasicum	*Elasmotherium caucasicum*
Elasmotherium sibiricum	*Elasmotherium sibiricum*
Elephas antiquus	*Palaeoloxodon antiquus*
	Paleoloxodon antiquus
Elephas planifrons	*Archidiskodon planifrons*
	Mammuthus planifrons
Eobison tamanensis	*Bison (Eobison) degiuli*
	Bison tamanensis
	Eobison degiulii
	Eobison suchovi
Eostyloceros blainvillei	*Eostyloceros blainvillei*
Eostyloceros pidoplitschkoi	*Eostyloceros pidoplitschkoi*
Eosyncerus ivericus	*Eosyncerus ivericus*
Equus abeli	*Equus abeli*
Equus altidens	*Equus granatensis*
	Equus marxi
	Equus stenonis granatensis
Equus apolloniensis	*Equus apolloniensis*
Equus ferus	*Equus caballus przewalskii*
	Equus antunesi
	Equus caballus
	Equus caballus mosbachensis
	Equus caballus przewalskii
	Equus chosaricus
	Equus germanicus
	Equus gmelini
	Equus insulidens
	Equus latipes
	Equus lenensis
	Equus mosbachensis
	Equus przewalskii
	Equus spelaeus
	Equus steinheimensis
	Equus transilvanicus
	Equus uralensis
	Equus taubachensis
Equus hemionus	*Equus hemionus*
Equus hipparionoides	*Equus hipparionoides*
Equus hydruntinus	*Equus graziosii*
Equus livenzovensis	*Plesippus athanasiui*
Equus major	*Equus bressanus*
	Equus robustus
	Equus stenonis major
	Plesippus (Allohippus) euxinicus
	Plesippus euxinicus
Equus namadicus	*Equus namadicus*
Equus petraloniensis	*Equus petraloniensis*
Equus senezensis	*Equus stehlini*
Equus stenonis	*Allohippus stenonis*
	Allohippus stenonis vireti
	Equus simionescui
	Equus stenonis mygdoniensis

	Equus stenonis senezensis
	Equus stenonis vireti
Equus suessenbornensis	*Equus sussenbornensis*
Equus tabeti	*Equus tabeti*
Eucladoceros ctenoides	*Cervus ctenoides*
	Cervus senezensis
	Eucladoceros senezensis
	Eucladoceros vireti
	Eucladoceros darestei
	Eucladoceros ertborni
	Eucladoceros falconeri
	Eucladoceros orticeros
	Eucladoceros senezensis vireti
	Eucladoceros tegulensis
	Eucladoceros teguliensis
	Euctenoceros senezensis
	Euctenoceros senezensis vireti
Eucladoceros dicranios	*Eucladoceros dichotomus*
	Eucladoceros sedgwicki
	Cervus dicranios
Eucladoceros giulii	*Eucladoceros giulii*
Eucladoceros mediterraneus	*Eucladoceros mediterraneus*
Eucladoceros tetraceros	*Eucladoceros tetraceros*
Eucyon odessanus	*Canis odessanus*
Gallogoral meneghinii	*Gallogoral meneghinii*
Gazella borbonica	*Gazella borbonica*
Gazella bouvrainae	*Gazella bouvrainae*
Gazella janenschi	*Gazella janenschi*
Gazella postmitilinii	*Gazella postmitilinii*
Gazella sinensis	*Gazella sinensis*
Gazella subgutturosa	*Gazella subgutturosa*
Gazellospira gromovae	*Gazellospira gromovae*
Gazellospira torticornis	*Gazella torticornis*
Giraffa camaleopardalis	*Giraffa camaleopardalis*
Hemibos galerianus	*Bos galerianus*
Hemitragus albus	*Capra alba*
	Hemitragus alba
Hemitragus bonali	*Hemitragus bonali*
Hemitragus cedrensis	*Hemitragus cedrensis*
Hemitragus orientalis	*Capra dalii*
Hipparion crassum	*Hipparion crassum*
Hipparion fissurae	*Hipparion fissurae*
Hipparion longipes	*Plesiohipparion longipes*
Hipparion malustenense	*Hipparion malustenense*
Hipparion tchicoicum	*Hipparion tchicoicum*
Hippopotamus amphibius	*Hippopotamus amphibius*
Hippopotamus antiquus	*Hippopotamus major*
	Hippopotamus tiberinus
	Hippopotamus georgicus
	Hippopotamus ex gr. H. amphibius
Homotherium crenatidens	*Homotherium hungaricus*
	Homotherium nestianus
	Homotherium sainzelli

	Megantereon crenatidens
Homotherium davitashvilii	*Machairodus davitashvilii*
Homotherium latidens	*Homotherium moravicum*
Hoploaceratherium belvederense	*Hoploaceratherium belvederense*
Hyaena prisca	*Hyaena prisca*
Kolpochoerus olduvaiensis	*Kolpochoerus olduvaiensis*
Korynochaerus provincialis	*Korynochaerus provincialis*
Leptobos elatus	*Bos elatus*
Leptobos etruscus	*Leptobos etruscus*
Leptobos furtivus	*Leptobos merlai*
Leptobos stenometopon	*Leptobos stenometopon*
Leptobos vallisarni	*Leptobos vallisarni*
Loxodonta exoptata	*Loxodonta exoptata*
Lycaon falconeri	*Vulpes (Xenocyon) falconeri*
	Xenocyon falconeri
Lycaon lycaonoides	*Canis falconeri*
	Xenocyon lycaonoides
	Canis lycaonoides
Lynx issiodorensis	*Felis issiodorensis*
	Lynx brevirostris
Lynx lynx	*Lynx lynx*
Lynx pardinus	*Felis (Lynx) spelaea*
	Lynx spelaea
	Lynx pardina
	Felis (Lynx) pardina
	Lynx pardina spelaea
Lynx shansius	*Lynx shansius*
Mammut borsoni	*Zygolophodon borsoni*
Mammuthus meridionalis	*Archidiskodon meridionalis*
	Archidiskodon tamanensis
	Mammuthus gromovi
	Mammuthus meridionalis meridionalis
	Mammuthus meridionalis tamanensis
	Archidiskodon gromovi
Mammuthus primigenius	*Elephas primigenius*
Mammuthus rumanus	*Mammuthus rumanus*
Mammuthus trogontherii	*Elephas wuesti*
	Mammonteus trogontherii
	Mammuthus chosaricus
Mammuthus trogontherii	*Mammuthus wuesti*
Megaloceros giganteus	*Megaceros dupuisi*
	Megaceros giganteus
	Megaloceros euryceros
	Megaceros euryceros
Megaloceros savini	*Dolichodoriceros savini*
	Dolichodoryceros savini
	Megaceros savini
Megalovis balcanicus	*Megalovis balcanicus*
Megalovis latifrons	*Megalovis latifrons*
Megantereon cultridens	*Megantereon megantereon*
Megantereon whitei	*Megantereon whitei*
Mitilanotherium inexspectatum	*Mitilanotherium inexspectatum*

Mitilanotherium martinii	*Macedonitherium martinii*
	Sogdianotherium kuruksaense
Nyctereutes donnenzani	*Nyctereutes donnenzani*
Nyctereutes megamastoides	*Nyctereutes megamastoides*
Nyctereutes tingi	*Nyctereutes tingi*
Omochoerus phacochoeroides	*Omochoerus phacochoeroides*
Oryx gazella	*Oryx gazella*
Ovibos moschatus	*Ovibos moschatus*
Ovibos pallantis	*Ovibos pallantis*
Ovis ammon	*Ovis ammon antiqua*
Pachycrocuta brevirostris	*Crocuta sinensis*
	Hyaena brevirostris
	Pachycrocuta robusta
	Palaeotragus priasovicus
Panthera gombaszoegensis	*Panthera onca gombaszoegensis*
	Panthera toscana
	Felis toscana
Panthera leo	*Felis spelaea*
	Panthera leo fossilis
	Panthera leo spelaea
	Panthera spelaea
Panthera pardus	*Felis pardus*
Parabos athanasiui	*Parabos athanasiui*
Parabos cordieri	*Parabos cordieri*
Parabos soriae	*Parabos soriae*
Paracamelus alexejevi	*Paracamelus alexejevi*
Paracamelus alutensis	*Paracamelus alutensis*
Paracamelus bessarabiensis	*Paracamelus bessarabiensis*
Paracamelus gigas	*Paracamelus gigas*
Paracamelus kujalnensis	*Paracamelus kujalnensis*
Paracervulus australis	*Paracervulus australis*
Parailurus anglicus	*Parailurus anglicus*
Parailurus hungaricus	*Parailurus hungaricus*
Parastrepsiceros sokolovi	*Parastrepsiceros sokolovi*
Pelorovis oldowayensis	*Pelorovis oldowayensis*
Plesiohipparion houfenense	*Hipparion houfenense*
Plesiohipparion rocinantis	*Hipparion crusafonti*
	Hipparion gracile rocinantis
	Hipparion moritorum
	Hipparion moriturum
	Hipparion rocinantis
Pliocervus kutchurganicus	*Pliocervus kutchurganicus*
Pliocrocuta perrieri	*Hyaena perrieri*
	Hyaena striata
	Pliocrocuta perrieri
	Crocuta perrieri
	Pachycrocuta pyrenaica
	Pliocrocuta pyrenaica
	Pliohyaena perrieri
	Crocuta perrieri
	Pliocrocuta perrieri
	Hyena brunnea
Pliotragus ardeus	*Deperetia ardea*

	Hesperidoceras merlae
	Megalovis ardeus
Pontoceros ambiguus	*Pontoceros ambiguus*
Praedamalis deturi	*Praedamalis deturi*
Praemegaceros dawkinsi	*Megaloceros dawkinsi*
Praemegaceros obscurus	*Megaceroides obscurus*
	Praemegaceros boldrini
	Megaloceros obscurus
Praemegaceros pliotarandoides	*Eucladoceros orientalis*
	Psekupsoceros orientalis
	Cervus pliotarandoides
Praemegaceros solhilacus	*Megaceroides solhilacus*
	Cervus solilhacus
	Megaloceros solhilacus
Praemegaceros verticornis	*Allocaenelaphus verticornis*
	Allocaenelephas arambourgi
	Cervus belgrandi
	Megaceroides verticornis
	Megaloceros verticornis
	Orthogonoceros verticornis
Praeovibos priscus	*Praeovibos priscus*
Praeovibos schmidtgeni	*Praeovibos schmidtgeni*
Procamptoceras brivatense	*Procamptoceras brivatense*
Procapreolus cusanus	*Capreolus cusanus*
	Cervus cusanus
	Procapreolus wenzensis
	Capreolus cusanoides
Procapreolus moldavicus	*Procapreolus moldavicus*
Propotamochoerus provincialis	*Propotamochoerus provincialis*
Protoryx heinrichi	*Protoryx heinrichi*
Pseudalces mirandus	*Pseudalces mirandus*
Rangifer tarandus	*Rangifer tarandus*
Rupicapra rupicapra	*Rupicapra rupicapra*
Rusa rhenana	*Dama rhenana*
	Cervus ischnoceros
	Cervus pardinensis
	Cervus perolensis
	Cervus philisi
	Cervus philisi philisi
	Cervus philisi valliensis
	Cervus rhenanus
	Dama pardinensis
	Metacervoceros rhenanus
	Metacervocerus pardinensis
	Pseudodama nestiii vallonnetensis
	Pseudodama perolensis
	Pseudodama rhenanus
Saiga tatarica	*Saiga tatarica*
Sinomegaceros tadzikhisanica	*Sinomegaceros tadzikhisanica*
Soergelia brigittae	*Soergelia brigittae*
Soergelia intermedia	*Soergelia intermedia*
Soergelia minor	*Soergelia minor*
Stephanorhinus leptorhinus	*Stephanorhinus leptorhinus*

Stephanorhinus etruscus	*Dicerorhinus etruscus*
	Dicerorhinus etruscus etruscus
Stephanorhinus hemitoechus	*Dicerorhinus hemitoechus*
	Stephanorhinus hemitoecus
Stephanorhinus hundsheimensis	*Stephanorhinus hundsheimensis*
Stephanorhinus jeanvireti	*Dicerorhinus jeanvireti*
	Dicerorhinus megarhinus
	Stephanorhinus elatus
	Stephanorhinus megarhinus
Stephanorhinus kirchbergensis	*Dicerorhinus kirchbergensis*
	Dicerorhinus merki
	Stephanorhinus mercki
Stephanorhinus miguelcusafronti	*Stephanorhinus miguelcusafronti*
Stephanorhinus pikermiensis	*Stephanorhinus pikermiensis*
Sus arvernensis	*Sus minor*
Sus scrofa	*Sus scrofa*
Sus sondaari	*Sus sondaari*
Sus strozzii	*Sus strozzii*
Tapirus arvernensis	*Tapirus minor*
Tetralophodon longirostris	*Tetralophodon longirostris*
Tragelaphus buxtoni	*Tragelaphus buxtoni*
Tragospira pannonica	*Tragospira pannonica*
Ursus arctos	*Ursus praearctos*
	Ursus rossicus
Ursus deningeri	*Ursus deningeri*
Ursus dolinensis	*Ursus dolinensis*
Ursus etruscus	*Ursus etruscus*
Ursus minimus	*Protarctos boeckhi*
	Ursus arvernensis
	Ursus boeckhi
	Ursus mediterraneus
	Ursus minimus-etruscus
	Ursus minutus
	Ursus pyrenaicus
	Ursus ruscinensis
	Ursus schertzi
	Ursus stehlini
	Ursus telonensis
	Ursus wenzensis
Ursus rodei	*Ursus rodei*
Ursus spelaeus	*Ursus spelaearctos*
Ursus thibetanus	*Ursus thibetanus*
Viretailurus schaubi	*Panthera schaubi*
Vulpes alopecoides	*Vulpes alopecoides*
Vulpes angustidens	*Vulpes angustidens*
Vulpes corsac	*Vulpes corsak*
Vulpes praecorsac	*Cynalopex praecorsac*
Vulpes praeglacialis	*Vulpes praeglacialis*
Vulpes vulpes	*Vulpes vulpes*
Xenalopex remenyii	*Xenalopex remenyii*

Literature cited for taxonomy

- Abbazzi, L., 2004. Remarks on the validity of the generic name *Praemegaceros* Portis 1920, and an overview on *Praemegaceros* species in Italy. Rend. Fis. Acc. Lincei, 15:115-132.
- Alberdi, M.T., E. Ortiz-Jaureguizar, M.L. Prado. 1998, A quantitative review of European stenonoid horses. Journal of Paleontology 72:371-387
- Azzaroli, A., 1979. Critical remarks on some Giant Deer (genus *Megaceros* Owen) from the Pleistocene of Europe. Palaeont. It. 71:5-16.
- Bajgusheva, T.S., V.V. Titov, A.S. Tesakov. 2001. The sequence of Plio-Pleiotocene mammals from the South Russian plain (the Azov Region). Bollettino della Società paleontologica Italian 40(2).
- Breda, M., M. Marchetti, 2005. Systematical and biochronological review of Plio-Pleistocene Alceini (Cervidae; Mammalia) from Eurasia. Quaternary Science Reviews 24:775-805.
- Brugal, J.P., R. Croitor. 2004. New insights concerning Lower Pleistocene cervids and bovids in Europe: dispersal and correlation. 18th International Senckenberg Conference, VI International Palaeontological Colloquium in Weimar: Late Neogene and Quaternary biodiversity and evolution: regional developments and interregional correlations, Weimar (Germany), 25th - 30th april 2004 : Conference Volume. L. C. Maul and R.-D. Kahlke: 84-85.
- Crégut-Bonnoure, E., 2006. European Ovibovini, Ovini and Caprini (Caprinae,Mammalia) from the Plio-Pleistocene: new interpretations. Courier-Forschungsinstitut Senckenberg 256:139-158.
- Crégut-Bonnoure, E., 2007. Apport des Caprinae et Antilopinae (Mammalia, Bovidae) à la biostratigraphie du Pliocène terminal et du Pléistocène d'Europe Quaternaire 18 :73-97.
- Crégut-Bonnoure, E., V. Dimitrijević, V. 2006, *Megalovis balcanicus* sp. nov. and *Soergelia intermedia* sp. nov. (Mammalia, Bovidae, Caprinae), new Ovibovini from the Early Pleistocene of Europe. Revue de Paléobiologie, 25:723-773
- Croitor, R., 1999. On systematic position of "moldavian sambar deer" from the Pliocene of Moldova. Bollettino della Società Paleontologica Italiana 38:87-96.

- Croitor, R., 2004. Systematics and phylogeny of large-sized deer of the genus *Praemegaceros Portis*, 1920 (Cervidae, Mammalia). 18th International Senckenberg Conference, VI International Palaeontological Colloquium in Weimar: Late Neogene and Quaternary biodiversity and evolution: regional developments and interregional correlations, Weimar (Germany), 25th - 30th april 2004: Conference Volume. L. C. Maul and R.-D. Kahlke: 89-90.
- Croitor, R., D.S. Kostopoulos. 2004. On the systematic position of the large-sized deer from Apollonia, Early Pleistocene, Greece Palaeontologische Zeitschrift 78:137-159.
- Di Stefano, G., C. Petronio. 2002. Systematics and evolution of the Eurasian Plio-Pleistocene tribe Cervini (Artiodactyla, Mammalia). Geologica Romana, 36, 311-334
- Duvernois, M.P., C. Guérin. 1989. Les Bovidae (Mammalia) du Villafranchien supérieur d'Europe occidentale.Géobios 22:339-379.
- Ficcarelli G., D. Torre. 1974. Nuovi reperti del gatto villafranchiano di Olivola. Atti Soc. Tosc. Sci. Nat., Mem., Serie A, 81:312-317.
- Fortelius M., P. Mazza, B. Sala, 1993 - *Stephanorhinus* (Mammalia: Rhinoceroitidae) of the western European Pleistocene, with a revision of *S. Etruscus* (Falconer, 1868). Palaeontographia Italica 80:63-155.
- García N., J.L Arsuaga. 2001. *Ursus dolinensis*: a new species of Early Pleistocene ursid from Trinchera Dolina, Atapuerca (Spain). C.R. Acad. Sci. Paris, Sciences de la Terre e des Planets 332:717-725.
- Kurtén B. 1968. Pleistocene mammals of Europe. Aldine Publishing Company, Chicago.
- Kurtén B. 1978. The Lynx from Etouaires, Lynx issiodorensis (Croizet & Jobert), late Pliocene. Ann. Zool. Fennici 15: 314-322.
- Lacombat, F., 2006. Pleistocene Rhinoceroses in Mediterranean Europe and in Massif Central (France). Courier- Forschungsinstitut Senckenberg 256:57-70.
- Lister, A.M., 1990. Taxonomy and Biostratigraphy of Middle Pleistocene Deer Remains from Arago, Pyrénées-Orientales, France in Les cervidés quaternaires. Quaternaire 1:225-230.
- Lister, A.M., A.V. Sher. 2001. The Origin and Evolution of the Woolly Mammoth. Science 294:1094-1097

- Martinez Navarro, B., M. Palombo. 2004. Occurrence of the Indian genus *Hemibos* (Bovini, Bovidae, Mammalia) at the Early-Middle Pleistocene transition in Italy. QUATERNARY RESEARCH 61:314-317.
- Martínez-Navarro B., L. Rook. 2003. Gradual evolution in the African hunting dog lineage. Systematic implications. C. R. Palevol 2:695-702.
- Made, J., van der, 1999. Ungulates from Atapuerca TD6. J Human Evolution 37:389-413.
- Martínez-Navarro, B., P. Palmqvist. 1996. Presence of the African saber-toothed felid *Megantereon whitei* (Broom, 1937) (Mammalia, Carnivora, Machairodontinae) IN Apollonia-1 (Mygdonia Basin, Macedonia, Greece).
- Mazza, P., M. Rustioni. 1994. On the phylogeny of Eurasian bears. Palaeontographica Abt. A 230:1-38.
- Monguillon, A., N. Spassov, A. Argant, K. Kauhala, S.Viranta. 2004. *Nyctereutes vulpinus* comb. et stat. nov. (Mammalia, Carnivora, Canidae) from the late Pliocene of Saint-Vallier (Drôme, France). Geobios 37(1):S183-S188.
- Morales J., D. Soria, P. Montoya, B. Perez, M.J. Salesa. 2003. *Caracal depereti* Nov. Sp. y *Felis aff. sylvestris* (Felidae, Mammalia) del Plioceno inferior de Layna (Soria, España). Estudios Geologico 59:229-247.
- Mousil R. 1968. Stranska Skala : its meaning for Pleistocene studies. Current Anthropology 9(5):534-539.
- O'Regan HJ., A. Turner. 2004. Biostratigraphic and paleoecological implications of new fossil felid material from the Plio-Pleistocene site of Tegelen, the Netherlands. Palaeontology, 47(5):1181-1193.
- Palombo M.R., B. Azanza, M.T. Alberdi. 2000-2002. Italian mammal biochronology from the latest Miocene to the middle Pleistocene: a multivariate approach. Geologica Romana 36:335-368.
- Pfeiffer, T., 1999, Die Stellung von Dama (Cervidae, Mammalia) in System plesiometacarpaler Hirsche des Pleistozäns-Phyllogenetische Rekonstruktion-Metrische Analyse. Courier Forsch. Senckenberg 211:1-218.
- Rohland, N., J.L. Pollack, D. Nagel, C. Beauval, J. Airvaux, S. Pääbo, M. Hofreiter. 2005. The population history of extant and extinct hyenas. Mol. Biol. Evol. 22(12):2435-2443.

- Rook, L. 1994. The Plio-Pleistocene Old World Canis (Xenocyon) ex gr. Falconeri. Boll. Soc. Paleontologica Italiana 33(1):71-82.
- Rook, L., Torre D. 1996. The latest Villafranchian, early Galerian small dogs of the Mediterranean area. Acta Zool. Cracoviense 39:427-34.
- Rook, L.1993. I cani dell'Eurasia dal Miocene superiore al Pleistocene medio. Tesi di Dottorato di Ricerca in Paleontologia, Università di Modena, Firenze , Bologna, Roma "La Sapienza".
- Rustioni, M., 1992. On Pliocene tapirs from France and Italy. Boll. Soc. Paleont. It., 31(3).
- Sardella, R. 1998. The Plio-Pleistocene Old World dirk-toothed cat *Megantereon* ex gr. *cultridens* (Mammalia, Felidae, Machairodontinae), with comments on taxonomy, origin and evolution. N. Jb. Geol. Paläont. Abh. 207(1):1-36.
- Sotnikova, M., P. Nikolskiy. 2006. Systematic position of the cave lion *Panthera spelaea* (Goldfuss) based on cranial and dental characters. Quaternary International 142-143:218-228.
- Testu, A. 2006. Etude paléontologique y biostratigraphique des Felidae et Hyaenidae pléistocènes de l'Europe méditerrannéenne. PhD thesis de l'Universite de Perpignan.
- Turner, A. 1987. Megantereon cultridens (Cuvier) (Mammalia, Felidae, Machairodontinae) from Plio-Pleistocene deposits in Africa and Eurasia, with comments on dispersal and the possibilità of a New World origin. Journal of Palaeontology 61(6):1256-1268.
- Turner, A., M. Antón. 1997. The big cats and their fossil relatives. Columbia University Press. New York.
- Vos, J. de, D. Mol,. J.W.F. Reumer. 1995. Early Pleistocene cervids from the Oosterschelde (The Netherlands) with a revision of the cervid genus *Eucladoceros* Falconer, 1868. Deinsea, 2:95-121.
- Werdelin, L. 1981. The evolution of lynxes. Ann. Zool. Fennici 18: 37-71.
- Werdelin, L., N. Solounias. 1991. The Hyaenidae: Taxonomy, systematics and evolution. Fossils and Strata 30:1–104.
- Zouhri, S., A. Bensalmia. 2005. Révision systématique des *Hipparion* sensu lato (Perissodactyla, Equidae) de l'Ancien Monde. Estudios Geol. 61:61-99.

APPENDIX B – LOCAL FAUNAL ASSEMBLAGES (LFAS) INCLUDED IN THIS STUDY. FOR EACH LFA, THERE ARE THE GEOGRAPHICAL COORDINATES AND A NUMERICAL AGE ESTIMATE. AGE WAS CALCULATED BY TAKING THE AVERAGE OF TWO INDEPENDENT ESTIMATES OBTAINED BY APPLYING ALROY'S ML AEO AND FORTELIUS ET AL.'S SPECTRAL ORDERING PROCEDURE

Locality name	Latitude	Longitude	Age
Virghis	46.11	25.53	3750636
Triversa (Villafranca d'Asti)	44.90	8.03	3616827
Lucheshty	45.30	29.00	3494827
Capeni	46.16	25.55	3400000
Malusteni	46.16	27.91	3400000
Varghis	46.46	25.40	3400000
Karboliya Beds	45.87	28.45	3388989
Kuchurgan gravel	47.00	30.00	3365419
Kossiakino 1	45.20	41.49	3357189
Iaras 2	45.86	25.60	3325036
Iaras 1	45.86	25.60	3247830
Hajnacka I/3	48.30	19.75	3223370
Gaville/Santa Barbara	43.40	12.80	3172319
Castelnuovo dei Sabbioni	43.34	11.37	3117526
Covrigi	44.71	23.16	3097535
Groserea	44.71	23.48	3047889
Kvabeby	42.00	46.00	3042690
Araci	45.80	25.55	3009814
Tulucesti	45.55	28.00	2971839
Sutto	47.71	18.31	2939829
Etuliya	45.25	29.00	2779168
Roccaneyra	45.91	3.33	2700000
Chagny	46.90	4.73	2473705
Vialette (Haute Loire)	45.11	3.83	2426252
Nova Vieska	47.87	18.45	2420896
Strekov	47.88	18.43	2420896
Cernatesti	44.43	23.43	2323708
Les Etouaires-Perrier	45.55	2.91	2319212

Villarroya	42.11	-2.06	2233817
Ercsi	47.25	18.90	2198605
Montopoli	43.06	10.75	2098803
Oosterschelde	51.55	4.00	2042637
Sesklon (SES)	39.37	22.93	2025537
Youkari-Sogutonu	39.81	30.40	2013735
Varshets	43.20	23.29	1985567
Saint-Vidal (Haute-Loire)	45.11	3.80	1978288
La Roche Lambert	45.36	3.60	1972363
Norwich Crag	52.20	1.60	1969301
Dove Holes	53.30	-1.89	1968649
Le Coupet (Haute-Loire)	45.13	3.55	1950000
La Pietris	44.75	23.92	1950000
Saint Vallier	45.17	4.82	1950000
Valea Graunceanului	44.75	23.91	1950000
Psekups	44.49	39.12	1950000
Pardines (Puy-de-Dome)	45.56	3.16	1942765
Costa San Giacomo (Anagni)	41.73	13.20	1939052
Chilhac 2, Haute-Loire	45.13	3.45	1926837
Flaauwerspolder	51.61	3.87	1905573
Erpfinger	48.31	9.30	1878887
Cornillet (Alpes de Haute Provence)	45.25	0.78	1877918
Seneze (Haute Loire)	45.25	3.50	1877236
Huelago	37.42	-1.81	1865705
Cava Toppetti (Todi)	42.78	12.40	1849517
Valle Catenaccio	41.73	13.20	1826844
La Puebla de Valverde	40.21	-0.91	1787358
Dmanisi A	41.30	44.15	1780000
Leu	44.18	24.00	1770573
Fintina lui Mitilan	44.65	23.93	1737214
Strmica	44.16	16.25	1719344
Tegelen	51.33	6.13	1703785
Gerakarou 1 (GER)	40.70	23.15	1664124
Fonelas	37.40	-3.16	1656847
Kos	36.25	27.25	1642636
Vassiloudi (VSL)	40.70	23.15	1609052

Valdarno sup.	43.53	11.58	1602451
Semibalki	47.00	39.01	1569976
Blassac-La-Gironde Haute-Loire	45.16	3.42	1537591
Livakos (LIV)	38.00	21.80	1497991
Matassino (Figline Valdarno)	43.62	11.47	1470541
Torre di Picchio	42.65	12.48	1463977
Pantalla (Umbria)	42.87	12.38	1455137
Casa Sgherri (Massarella)	43.73	10.80	1449407
La Sartanette (Porche d'Entree)	43.93	4.57	1441959
Olivola	44.22	10.02	1428505
Casa Frata	43.62	11.47	1423415
Poggio Rosso (Mugello)	43.61	11.45	1416981
Halykes, Magnesia	39.20	22.80	1410169
Il Crostolo	44.55	10.42	1407906
Fintina Alortitei	44.75	23.91	1397665
Valdarno sup. (Tasso FU)	43.53	11.58	1372519
Fontana Acetosa	41.73	13.20	1366132
Selvella (Pievepelago)	44.20	10.62	1328647
Bacino Tiberino	43.47	12.40	1308286
Leffe (Lower level)	41.90	12.25	1302143
Monte Riccio (Tarquinia)	42.25	11.75	1286427
Faella	43.68	12.48	1276058
Pirro Nord	41.78	15.45	1244532
Pietrafitta	42.98	12.25	1219639
Llobregat	41.20	-2.20	1215741
Ceyssaguet	45.11	3.90	1200000
Durfort (Gard)	43.91	3.95	1188915
Mugello (fluviolacustrine phase, Barberino)	44.00	11.25	1164694
Madonna della Strada (Scoppito, Aquila)	42.37	13.25	1163320
Val di Chiana (Farneta FU) Toscana	43.22	11.85	1134453
Redicicoli (Roma)	41.93	12.52	1104166
Colle Curti (Colfiorito)	42.95	12.92	1100000
Saint Prest (Chatres)	48.45	1.50	1026648
Sainzelles (Haute Loire)	45.66	3.90	991410
Barranco Leon 5	37.70	-2.44	985046
Venta Micena	37.73	-2.70	983000

Noordzee II	52.47	4.62	947694
Mestas de Con	43.33	-5.00	927807
Cullar de Baza- 1 Granada	37.60	-2.57	913289
Rotbav-Dealul	45.81	25.55	759352
Imola	44.35	11.70	756284
Grotte de la Martine	44.78	1.22	700000
Betfia 5	46.96	22.03	678568
Maasvlakte 1	51.09	4.07	630876
Suessenborn	50.98	11.38	611546
Mosbach 1	50.40	8.16	535517
Ponte Galeria 2	41.82	12.30	507899
Voigtstedt	51.40	11.31	498986
Jockgrim, Pfalz	49.16	8.30	483497
Borgonuovo (Siena)	43.22	11.90	481507
Betfia 7 4a	46.96	22.03	467905
Mauer bei Heidelberg	49.33	8.81	443703
Tiraspol	46.83	29.60	421620
Feldioara-Cariera	46.41	23.86	413118
Chlum	49.40	16.80	410224
Miesenheim 1	50.48	7.45	407855
Corton	52.45	1.73	405174
Monte Tenda (Soave, Verona)	45.40	11.25	403496
West Runton freshwaterbed	52.93	1.23	400705
Wurzburg-Schalksberg	49.82	9.95	400646
Pakefield rootlet bed	52.45	1.71	388968
Randersacker, Würzburg	49.85	9.97	382530
Isernia La Pineta	41.60	14.23	382096
Terra amata (Alpes Maritimes)	43.70	7.20	380000
Verchiezeuil (Saone et Loire)	47.15	-0.30	370342
Viatelle	45.25	11.15	368857
Koneprusy C718 bei Karlstejn	49.93	14.83	367932
Azykh, layer 5	39.32	45.37	364000
Nikolskoe (Volga)	47.80	46.40	364000
Rajgorod	48.40	44.95	364000
Tsona cave	42.00	43.24	364000
Monte Oliveto (Siena province)	43.20	11.53	360470

Furninha	39.36	-9.37	355509
Lunel-Viel, Hérault	43.66	4.07	354631
Montmaurin	43.21	0.63	350159
Larissa	39.38	22.25	335162
Campoverde (Aprilia_Latina)	41.58	12.65	312486
N. Chalkidiki (Central Macedonia)	40.60	23.50	308977
Levallois (Region Parisienne)	48.90	2.30	308977
Megalopolis basin (Peloponnese)	37.40	22.13	308818
Valdemino (Borgio Verezzi)	44.15	8.30	308655
Grotte d'Aldene, Couche K (Herault)	43.33	2.71	283729
Prezletice	50.19	14.60	283688
Lubni	50.00	33.00	271500
Contrada Monticelli (Castellana)	40.88	17.10	268324
Bruges (Pres de Bordeaux)	44.87	-0.60	268164
Bear's Cave (Upper Galilee)	32.85	35.07	250000
Orgnac 3 (Ardeche)	44.30	4.43	248612
Notarchirico	40.95	15.82	247575
Atapuerca TG10A	42.33	-3.50	246500
Atapuerca TG11	42.33	-3.50	246500
Castel di Guido	41.90	12.30	245582
Fontana Ranuccio (Anagni)	41.73	13.20	245183
Chernyj Jar(Nizhnee Zajmishch)	48.05	46.05	243500
Galeria Pesada (Almonda)	39.50	-8.61	241000
Weimar-Ehringsdorf LT	50.98	11.31	235000
Hunas st E-F	49.50	11.55	215000
Weimar-Ehringsdorf UT	50.98	11.31	192000
Tunguz peninsula	54.00	48.50	178500
Grotte du Lazaret CII (Nice)	43.70	7.30	170000
Cova Negra IV	38.96	-0.47	157500
La Parte	42.00	-1.00	150000
Visogliano (Duino Aurisia)	45.77	13.63	135399
Mosbach 2	50.40	8.16	131306
Hunas Riss	49.50	11.58	130000
Wolfskehlen	49.87	8.51	126869
Zemst IIB	50.99	4.39	126200
Grabschutz	51.47	12.28	125645

Aveley	51.50	0.27	124932
Lehringen	52.87	9.39	124932
Kirkdale cave	54.27	-0.92	124830
Joint Mitnor cave	50.48	-3.77	124728
Velica Pecina k	46.29	16.04	124422
Rabutz	51.43	12.18	124320
Taubach	50.95	11.37	124320
Barrington	52.12	0.03	124014
Trafalger Square	51.50	-0.17	123708
Bruehl 1	49.38	8.50	123606
Poroslyuk	48.33	20.53	123606
Crumstadt 1	49.82	8.53	123403
Burgtonna	51.13	10.62	123199
Gross Rohrheim	49.70	8.46	122995
Kalman Lambrecht cave	48.17	20.58	122791
Crayford	51.45	0.18	122689
Marsworth	51.82	-0.64	122587
Zaskal'naya	45.00	34.00	122500
Stuttgart - Unterturkheim	48.75	9.23	122383
Kopanovka	47.50	46.80	122179
Luttenberg	52.42	6.45	121873
Neumark Nord	51.33	11.87	121160
Eich	49.75	8.43	120752
Stockstadt	49.01	8.44	120140
Veternica j	45.84	15.87	120038
Leeheim	49.85	8.40	119529
Shkurlat	50.00	40.80	110558
Binagady	40.50	49.50	98000
Kiik-Koba	44.97	34.42	97000
Azykh	39.32	45.37	90000
Matuzka l. 3-7	44.60	39.60	90000
Quisisana, Capri	40.91	14.37	88630
Hunas st. D	49.50	11.55	88500
Boxgrove	50.85	-0.71	87514
Grotta Romanelli	40.10	18.43	87354
Caune de L'Arago CM I (Pyrenees)	42.80	2.75	82250

Steinheim middle level	48.58	9.16	82250
La Solana del Zamborino, Granada	37.57	-2.91	81931
Casal De' Pazzi (Rebibbia)	41.92	12.57	81612
Heppenloch	48.53	9.51	81453
Montignoso	44.00	10.16	81453
Bucine (Arezzo)	43.47	11.62	81293
Malagrotta (Roma province)	41.88	12.18	81134
Devil's Tower	36.22	-5.50	80974
Purfleet gravels	51.43	0.30	80974
Mezmaiskaya Cave 2B	45.00	39.00	80815
Cueva de los Huesos	40.90	-0.71	80655
Pech de l'Aze, Couche 9 (Dordogne)	44.87	1.25	80655
La Polledrara di Cecanibbio	41.90	12.25	80655
Sedia Del Diavolo	42.00	12.62	80655
Torre In Pietra (Upper Beds)	41.92	12.20	80655
Grotta Cola	42.00	0.83	80496
Pontecorvo (Frosinone)	41.45	13.70	80336
Abri Caminade-Ouest	44.85	1.27	80177
Cerveteri (Rome)	41.98	12.10	80177
Fara Sabina	42.22	12.73	80177
Caune de L'Arago CM III (Pyrenees)	42.80	2.75	80017
Ambrona	41.15	-2.50	80017
Bivak cave Wurm	47.63	18.92	80000
Jaskinia Raj	50.83	20.50	80000
Caune de L'Arago, Complexe Sommital (Pyrennes)	42.80	2.75	79858
Andreevka	49.00	32.00	79858
Châtillon-Saint-Jean, Dròme	45.04	5.07	79858
Maar de Saint Hippolyte	45.91	3.05	79858
Riano	42.10	12.52	79858
San Sidero	40.11	18.30	79858
Volax (E. Macedonia)	41.31	24.00	79858
Alkhast	43.30	47.00	79698
Bilzingsleben II	51.30	11.07	79698
Prati Fiscali	41.92	12.50	79698
Riparo Predastel	46.20	11.16	79698
Zejukovo, Nal'chik	45.60	43.00	79698

Cleon	49.30	1.03	79539
Los Torrejones	41.00	-3.25	79539
Los Casares B (Guadalajara)	40.95	-2.28	79379
Monte Delle Gioie	41.93	12.50	79379
Pinilla del Valle, Madrid	40.91	-3.81	79379
Brecce di Soave	42.45	11.25	79220
Ingarano d/e	41.77	15.65	79220
Villacastin C2	40.80	-4.37	79220
Vitinia (Upper Beds) (Roma province)	41.78	12.40	79220
Buca della Iena	43.93	10.33	79060
La Grotte des Fees	45.03	0.50	79060
Horvolgy	48.50	20.30	79060
Torre In Pietra (Lower Beds)	41.92	12.20	79060
Pech de l'Aze, Couche 4 (Dordogne)	44.87	1.25	79000
Baume de Gonvillars (Becanson)	47.25	6.00	78901
Cueva del Congosto, Guadalajara	40.87	-3.33	78901
Mezmaiskaya Cave 1–2	45.00	39.00	78901
Grotta Perin	45.28	11.36	78901
Petralona (Chalkidiki)	40.37	23.15	78901
Cannstatt I	48.79	9.18	78741
Icoana	44.42	24.71	78741
Abri du Morin A4	44.82	0.09	78741
A. Rousseau [Dousse]	46.71	0.87	78741
Zoppenga 1	45.42	11.25	78741
Bristie 1	45.73	13.73	78582
Sveduv Stul 12	49.27	16.70	78582
Montagne de Girault [Genay]	47.53	4.28	78500
Grotta Azzurra	45.90	13.70	78422
Grotta Benussi	45.67	13.75	78422
Montousse I (Haute Pyrenees)	43.11	0.37	78422
Artenac 10	45.63	0.15	78263
Gabrovizza	45.72	13.70	78263
Grotta San Leonardo	45.73	13.73	78263
Mezmaiskaya Cave 2A	45.00	39.00	78263
Abri du Morin B1	44.82	0.09	78263
Riparo Mezzena	45.30	10.59	78263

Singil	47.02	47.44	78263
Soave	45.42	11.25	78263
Agios Georgios	41.05	22.50	78103
Bettenroder Berg 14	51.47	10.02	78103
Biache Saint Waast (Pas de Calais)	50.90	1.90	78103
Castillo	43.28	-3.95	78103
Drama basin (E. Macedonia)	41.40	24.20	78103
Trou Reuviau-a-Furfooz	50.21	4.97	78103
Abìmes de la Fage, Corrèze	44.08	1.51	77944
Hortus Grotte	43.80	3.87	77944
Gr. de la Nauterie I [La Romieu]	44.01	0.50	77944
Quinzano	45.27	11.00	77944
Roter Berg	50.64	11.42	77944
Sternatia	40.22	18.22	77944
Abri des Battus 5	44.08	1.72	77784
Abri de Campalou	45.07	5.23	77784
Pestera la Adam29	44.42	28.52	77784
Riparo Tagliente	45.31	10.59	77784
Grotte di Veja A	45.61	10.95	77784
Grotte di Veja C	45.61	10.95	77784
La Roche Cotard [37 - Langeais]	47.34	0.43	77625
Covoli di Velo	45.65	11.20	77625
Kosh-Koba	44.95	34.40	77500
Apidima Cave C	37.00	22.58	77465
Dafnero (Haliakmon basin)	40.19	21.52	77465
Bau de l'Aubesiere, Couche 4 (Vaucluse)	43.80	5.30	77306
Bau de l'Aubesiere, Couche IH (Vaucluse)	43.80	5.30	77306
Cueva de Ermittia	43.18	-2.10	77306
Las Figuras (Alcorlo)	41.01	-3.01	77306
Cueva Millan 1a	42.05	-3.47	77306
Neapolis (Haliakmon basin)	40.30	21.36	77306
Grotte Scladina1A	50.43	5.00	77306
Castelcivita	40.50	15.24	77146
Grotta del Cerè	45.37	11.20	77146
Abri du Flageolet I	44.84	1.08	77146
Grotta Tilde	45.71	13.71	77146

Bacho Kiro	42.94	25.42	76987
Grotta Maggiore	45.32	11.33	76987
Schweizerbild 4	47.70	8.63	76987
Trou du Docteur	50.59	5.21	76987
Gr. Velars Etrigny	46.58	4.81	76987
Cueva de Abauntz	43.08	-1.34	76827
Baume Moula-Guercy IV ~ Soyons (Ardeche)	44.88	4.84	76827
Budospest	48.12	20.65	76668
Maastricht-Belvedere 4	50.83	5.68	76668
Grotte Maldidier	44.82	1.18	76668
Artenac 8	45.63	0.15	76508
Abri des Battus 3	44.08	1.72	76508
Waterhall farm (Hertford)	51.48	0.05	76508
Apidima Cave B	37.00	22.58	76349
Ariendorf	50.53	7.30	76349
Bacon hole	51.26	0.18	76349
Carriere Fournier, Chatillon-Saint-Jean (Drome)	45.83	5.11	76349
Trou du Renard	43.44	6.24	76349
Villa Seckendorff-Bad Cannstatt	48.80	9.22	76349
Bocksteinschmiede f/h	48.55	10.15	76189
Kilkis (Central Macedonia)	41.05	22.87	76189
Shandon Cave	52.10	-7.63	76189
Bocksteinschmiede g=IV	48.55	10.15	76030
Steinheim upper level	48.58	9.16	76030
Akhshtyrskaja cave Mouster	43.50	40.17	75929
Bocksteinschmiede h/Höhle=IIIb	48.55	10.15	75870
Große Schulerloch C	48.93	11.83	75870
Kogelstein	48.37	9.72	75870
Monte Cucco	43.19	12.44	75870
Mauern Weinberghoehlen F	48.77	11.05	75870
Picken's Hole, Layer 5	51.29	-2.88	75711
Artenac 6	45.63	0.15	75551
Buchenloch	50.23	6.65	75551
Saint Eulaile	44.60	1.87	75551
Gr. di Sant'Agostino	41.22	13.51	75551
Grotte du Tai C"	45.07	5.25	75551

Goyet Cave st.4	50.43	5.02	75500
Maastricht-Belvedere 5	50.83	5.68	75500
Noordzee III	52.47	4.62	75500
Prolom 2 cave	45.00	34.60	75500
Starye Duruitory I.3-4	47.98	27.50	75500
Staryj Kodak	48.50	35.40	75500
Trinka II.3-4	48.00	26.90	75500
Cueva de Altamira Sol	43.40	-4.10	75392
Maasvlakte 2	51.09	4.07	75392
Grotta Pocala	45.73	13.67	75392
Rotselaar	50.96	4.72	75392
Grotte Scladina4A	50.43	5.00	75392
Zhiliche Sokola, 2	59.35	60.00	75232
Große Ofnethöhle IV	48.82	10.45	75232
Dorog	47.72	18.72	74913
Abri du Flageolet II	42.86	1.59	74913
Dendermonde	51.04	4.10	74754
Mezmaiskaya Cave 2	45.00	39.00	74594
Pestera la Adam16	44.42	28.52	74594
Pestera la Adam26	44.42	28.52	74594
Gr. de Preletang [Presles]	45.09	5.43	74594
Große Ofnethöhle V	48.82	10.45	74435
Niederleme	47.50	8.37	74435
Princesse_Pauline	50.50	5.03	74435
Brillenhohle	48.41	9.77	74116
Abri de la Madeleine	44.97	1.02	73797
Baume Moula-Guercy V-VII ~ Soyons (Ardeche)	44.88	4.84	73637
Remete cave	47.75	19.05	73637
Raj cave 6	50.87	20.57	73318
Grotte Scladina5	50.43	5.00	73318
Ztiny cave	49.27	16.67	73159
Schweizerbild 5	47.70	8.63	72840
Teufelsbrücke 2-3b	50.62	11.40	72680
Pestera Climente	44.59	22.26	72521
Romualdo Cave	45.37	13.67	72361
Willments gravels	51.46	-0.03	72361

Stellmoor	53.64	-0.21	72042
Swanscombe	51.43	0.28	72042
Wretton	52.57	0.48	72042
Brillenhohle	48.41	9.77	71883
Teufelsbrücke 3	50.62	11.40	71883
Usolcevskaya cave	59.23	62.00	71723
Kaninskaya cave	61.80	58.21	71085
Valea Sesii	46.91	22.54	71085
Climauti II i	47.50	28.50	70767
Burmantovo1, 2	61.27	60.50	70607
Teufelsbrücke 2-3a	50.62	11.40	70607
Jaskinia Nietoperzowa	50.22	19.77	70600
Torrente Conca (Morciano di Romagna)	43.92	12.65	70288
Rusenschloss	48.41	9.80	70129
Chokurcha I cave	45.00	33.77	70000
Oliveira Cave	39.53	-8.59	70000
Upton Warren gravels	52.31	-2.10	69810
Uninskaya	61.83	58.60	69172
Abri de Combe-Cullier	44.84	1.56	68693
Lebiazhenskoe	49.60	41.90	68215
Große Schulerloch E-F	48.93	11.83	67417
King Arthur's Cave	51.84	-2.66	67098
Kamen' Pisany	59.85	57.57	66779
Ushminskaya cave (stratum 1-2)	60.80	56.00	66779
Lynford	52.50	0.67	65500
Herdengelhoehle	48.84	14.97	64800
Barova cave	49.40	16.67	62500
Hofstade I	50.99	4.50	62500
Jaskinia Niedwiedzia	50.23	16.90	62500
Sirgenstein cave	48.40	9.77	62500
Veternica cave i	45.84	15.87	62500
Wildenscheuer cave st. I-II	50.42	8.13	62500
Combe Grenal [Domme, Dordogne]	44.81	1.22	62000
Barakaevskaya stoyanka	44.20	40.85	60000
Dakhovskaja cave	44.90	40.00	60000
Igrita cave	47.20	22.37	60000

Mamat-Koba	45.25	33.87	60000
Sukhaja Mechetka l.4	48.40	44.30	60000
La Roquette II [Conquerac]	43.94	3.90	57200
Fonseigner [Bourdeilles]	45.34	0.61	56400
Staroselje	44.67	33.85	56000
Le Moustier	45.00	1.07	55800
Los Moros I [Gabasa]	42.02	-0.40	54740
Gr. Guattari	41.23	13.10	54200
Kulna Cave	49.41	16.75	54143
Regourdou [Montignac]	45.06	1.17	53978
Das Geissenklosterle	48.40	9.77	52700
Istallosko cave	48.07	20.41	52049
Pin Hole Cave	53.26	-1.20	51561
La Chapelle-aux-Saints	45.00	1.73	51500
Erd	47.39	18.89	51410
Subalyuk	47.97	20.47	50000
Soldier's Hole	51.28	-2.77	48554
Pestera Cioarei	45.13	23.02	48350
Erevanskaja cave	40.50	44.51	47800
Abric Romani	41.54	-1.68	45437
Niederweningen	52.30	13.33	45000
Gr. Neron [Soyons]	44.89	4.84	44854
Kudaro 1, l.3	42.50	43.50	44150
Trou Magrite	50.21	4.97	43760
Brean Down	51.32	-3.02	43730
Crvena Stijena	42.78	18.50	43730
Banwell Bone Cave	51.32	-2.87	43244
Reclau Viver	42.16	-2.75	43047
Castillo	43.28	-3.95	42947
Gr. del Broion	45.47	11.57	42224
Coygan Cave	51.76	-4.50	41954
Combe Grenal [Domme, Dordogne]	44.81	1.22	41931
Castlepook Cave	52.22	-8.58	41631
Sclayn Cave	50.49	5.05	41569
Gr. di Paina	45.42	11.49	40843
Tokod	47.72	18.66	40600

Das Geissenklosterle	48.40	9.77	39059
Ilskaja 1&2	45.00	37.80	39000
Isturitz [Isturits]	43.37	-1.20	38896
Certova Pec (Radosina)	48.55	17.93	38400
Grotte de Cres (Var)	43.00	2.95	38315
Smolucka Pecina	43.53	20.37	38000
Caune de Belvis [Belvis]	42.85	2.06	37905
Abri Caminade [Caneda]	44.88	1.26	37894
A. Castanet [Sergeac]	45.01	1.10	37716
Krems-Hundssteig	48.41	15.59	37404
Camiac[-et-St-Denis]	44.79	-0.27	36986
Valina	43.48	-7.31	36700
La Quina Y-Z [Villebois la Valette]	45.50	0.30	36543
Abri Fumane	45.57	10.90	36463
Esquicho-Grapaou	43.93	4.33	36448
Abri Caminade [Caneda]	44.88	1.26	36366
Mollet Cave	42.16	-2.75	36260
Picken's Hole, Layer 3	51.29	-2.88	36197
Bacho Kiro	42.94	25.42	36184
Trou Magrite	50.21	4.97	36176
Das Geissenklosterle	48.40	9.77	36169
Lommersum	50.70	6.80	36163
Ermitons Cave	42.27	2.61	35968
Tata	47.63	18.35	35940
Gr. Tournal (or Grande Grotte de Bize) [Bize-Minervois]	43.34	2.88	35914
Pod Hradem Cave	49.39	16.72	35409
Szeleta Cave	48.12	20.63	35127
Les Cottes [St. Pierre de Maille]	47.70	0.85	34999
Abri Fumane	45.57	10.90	34939
Roche a Pierrot [St.-Cesaire]	45.75	-0.51	34670
Roc de Combe4	44.77	1.33	34544
Castelcivita	40.50	15.24	34540
Abri Pataud	44.93	1.00	34480
Hohlenstein-Stadel [IV]	48.55	10.17	34365
Shaitanskaya, 1 (stratum 3)	60.42	60.22	34310
Abri Fumane	45.57	10.90	34276

Velica Pecina j	46.29	16.04	33850
Grotte du Renne, Arcy-sur-Cure	47.60	3.77	33825
Risovaca	44.29	20.59	33800
Sirejol [Gignac]	45.00	1.47	33800
Les Cottes [St. Pierre de Maille]	47.70	0.85	32979
Les Rivaux, Loc. 1 [Espaly-St-Marcel]	45.06	3.87	32903
Figueira Brava Cave	38.49	-8.97	32878
La Quina Y-Z [Villebois la Valette]	45.50	0.30	32659
Trou Al'Wesse	50.42	5.29	32560
Krapina	46.18	15.89	32461
Willendorf II	48.32	15.40	32187
Vogelherd Cave	48.56	10.20	32122
Gross Weikersdorf C	48.28	15.58	32000
Paviland Cave [Goat's Hole]	51.55	-4.24	31717
Grotte Chauvet	44.39	4.42	31679
Gr. de La Baume [Gigny sur Suran]	46.48	5.48	31389
Schnurenloch	46.68	7.44	31344
Trou Walou	50.59	5.72	31333
Roc de Combe1c	44.77	1.33	31329
Zafarraya Cave	36.95	-4.13	31279
Jaurens [Nespouls]	45.07	1.52	31109
Milovice I	48.84	16.73	30939
Bacho Kiro	42.94	25.42	30901
La Ferrassie	44.96	0.94	30782
Grotte de Courau (Grotte Saucet) [St-Pe-de-Bigorre]	43.11	-0.16	30778
Columbeira	39.30	-9.19	30660
Robin Hood's Cave	53.27	-1.19	30240
Kent's Cavern	50.46	-3.50	30185
Cheremukhovo 2, 3	60.24	60.03	30140
La Salpetriere [Remoulins]	43.95	4.54	30119
Pego do Diabo	38.90	-9.22	30106
Abri Pataud	44.93	1.00	29900
Gorham's Cave	36.13	-5.30	29544
Abri du Facteur	44.98	1.06	29494
Caldeirao Cave	39.64	-8.46	29358
Tornewton Cave	50.49	-3.66	29176

Amalda Cave	43.23	-2.01	28936
Le Flageolet I [Bezenac]	44.85	1.08	28595
Roc de Combe7a	44.77	1.33	28550
La Ferrassie	44.96	0.94	28545
Abri Pataud	44.93	1.00	28516
A. du Mas Viel [St-Simon]	44.72	1.85	28435
Predmosti	49.43	17.44	28366
L'Ermitage [Lussac-les-Chateaux]	46.38	0.72	28313
Montagne de Girault [Genay]	47.53	4.28	28240
Cueto de la Mina	43.42	-4.84	28147
Kostienki XIV [Markina Gora]	51.39	39.04	28143
La Baume Longue [Dions]	43.93	4.31	28073
Gr. Paglicci	41.68	15.58	27952
Trou du Rhinoceros [St-Pe-de-Bigorre]	43.11	-0.16	27931
Bockstein-Torle	48.55	10.15	27876
Le Flageolet I [Bezenac]	44.85	1.08	27870
Pontnewydd Cave	53.23	-3.48	27815
Dolni Vestonice I	48.87	16.64	27734
L'Arbreda	42.16	-2.75	27712
Beckford	52.02	-2.04	27650
Krems-Wachtberg	51.50	17.00	27450
Cheremukhovo 4 (stratum 2)	60.24	60.03	27350
Le Piage [Fajoles]	44.80	1.37	27088
Le Piage [Fajoles]	44.80	1.37	27088
Maisieres-Canal	50.47	3.99	26885
Roc de Combe6	44.77	1.33	26839
Gr. du Spy	50.48	4.67	26775
Gr. del Fossellone	41.23	13.08	26750
Pavlov I	48.87	16.69	26730
Fontenioux [St Pierre de Maille]	46.70	0.86	26728
Les Pecheurs [Casteljau]	44.41	4.21	26455
Herdengelhoehle s.6	48.84	14.97	26235
Sungir'	56.13	40.48	25848
Le Flageolet I [Bezenac]	44.85	1.08	25752
Tuto de Camalhot [St-Jean de Verges]	43.01	1.63	25695
Gr. d'Echenoz-la-Meline [La Baume]	47.61	6.14	25677

Smorgon late Pleist	54.30	27.00	25550
Aitzbitarte III	43.27	-1.90	25466
Les Cottes [St. Pierre de Maille]	47.70	0.85	25114
Pilisszanto 1	47.67	18.90	25000
Molodova V [Kosoutsy]	48.27	27.28	24854
Gmelinskaja Kostienki 21 lower	50.96	39.70	24850
Salemas	38.89	-9.19	24820
Gr. de la Princesse [Marche-les-Dames]	50.48	4.97	24664
Akhshtyrskaja cave, Akhshatyr	43.50	40.17	24500
Solutre [O/A]	46.30	4.73	24411
Gr. St-Marcel [d'Ardeche] [Bidon]	44.33	4.54	24243
Abri Pataud	44.93	1.00	24045
Canecaude I [Villardonel]	43.31	2.34	24025
La Ferrassie	44.96	0.94	23662
Khotylevo II	53.34	34.12	23660
Berdyzhskaja stojanka	52.50	31.00	23400
Wildenscheuer cave st. III	50.42	8.13	23300
Cavallo	40.15	17.96	23151
Adler cave	49.25	16.67	23000
Avdeevskaja	51.10	36.00	23000
Devis-Khvreli cave	42.30	41.50	23000
Dovginichi	50.05	27.90	23000
Goyet Cave 3	50.43	5.02	23000
Gvardzhilas-Klde	42.00	42.50	23000
Hofstade III	50.99	4.50	23000
Jamburg	48.50	35.50	23000
Kanev	49.45	31.28	23000
Kharkov	50.00	36.20	23000
Ochoz cave	49.33	16.75	23000
Pekarna cave	49.25	16.67	23000
Pogorilivka	52.00	31.60	23000
Sakazhija	41.70	42.50	23000
Starye Duruitory I.1 upper	47.98	27.50	23000
Veternica cave e	45.84	15.87	23000
Veternica cave f	45.84	15.87	23000
Zhuravka	50.50	32.50	23000

Gr. d'Enlene [Montesquieu-Avantes]	43.06	1.20	22827
Gr. de Laraux	46.40	0.72	22696
Moravany-Lopata II	48.61	17.89	22630
Kulna Cave	49.41	16.75	22603
Climauti II S	47.50	28.50	22600
Gr. des Cottier[s] [Retournac]	45.21	4.01	22383
La Riera	43.42	-4.84	22280
Ekain Cave	43.16	-2.26	22220
Roc de la Melca	45.04	-0.49	22218
Laugerie-Haute Est	44.97	0.95	22207
Gr. des Bisons [Lurbe-St-Christau]	43.11	-0.60	22166
Ciuntu	48.24	27.04	22100
Mezinskaja	51.60	32.50	22050
Gura Cheii-Rasnov	45.54	25.48	22000
La Riera	43.42	-4.84	21765
Langmannersdorf A	48.24	15.88	21591
Gr. de La Baume d'Oullins (a.k.a. d'Oulen") [Labastide-de-Virac]	44.35	4.47	21508
Cueva Morin	43.36	-3.84	21499
Laugerie-Haute Ouest	44.97	0.95	21466
Abri Moula [Soyons]	44.89	4.84	21442
La Balme d'Epy [Jura]	46.38	5.43	21379
Balla cave	48.02	20.53	21344
Kostienki I, l.1	51.29	39.00	21308
Kastritsa	39.42	20.50	20800
Arene Candide	44.20	8.32	20470
Zarajsk	54.77	38.88	20450
Le Piage [Fajoles]	44.80	1.37	20167
Grubgraben	48.14	15.53	19380
Deszczowa Cave	50.53	19.50	19250
Shaitanskaya, Shaitanskaya cave, 1 (stratum 2)	60.42	60.22	19140
A. Combe Sauniere [Sarliac-sur-l'Isle]	45.23	0.88	18517
Spadzista St. A	50.05	19.92	18427
Pecine u Brini East&West caves	43.83	16.17	18388
Gr. Pegourie [Caniac du Causse]	44.62	1.66	18388
Anetovka II	44.10	39.00	18040

Cueva de Aitzbitarte	43.18	-2.10	17950
Kamenika	45.20	17.58	17500
Pecina na Gradini	45.33	14.50	17500
Zarilac	45.42	17.88	17500
Cosauti	48.19	27.21	17200
Cueva de Urtiaga	43.18	-2.10	17050
Vraona cave (Attiki)	37.92	23.90	16933
Zupanov Spodmol	45.32	14.50	16780
Cueva de Eralla	43.11	-2.05	16270
Medvezhaya cave (greyish-brown “B’’ loamy soil)	62.20	59.00	16130
Zawalona cave	50.06	19.80	15990
Mezherich	49.65	31.50	15950
Sandalja b	44.86	13.83	15790
Don settlements	49.00	41.00	15500
Klithi	40.17	20.10	15000
Novgorod-Severskij	52.00	33.15	15000
Chulatov (Chulatovo I)	52.40	32.00	14700
Gontsy	50.10	33.00	14365
Medvezhaya cave (greyish-brown “A” and grey loamy soil)	62.20	59.00	13260
Kakva-4	59.35	60.00	12800
Kopacina	43.60	16.90	12393
Chinchon I	43.91	5.08	12000
Mamutowa Cave	50.08	19.92	12000
La Laouza [Sanilhac-et-Sagries, Gard]	43.93	4.41	9568
Kasslerloch	47.75	16.00	8700
Jägerhaus 8e	48.05	8.98	8617
Siebenlinden	48.47	8.93	8540
Lisia	60.25	60.05	6193
Akhshtyrskaja cave Hol, Akhshatyr	43.50	40.17	5000
Belaja cave Kolkhida Hol	42.32	42.62	5000
Burghöhle_Dietfurt Hol	48.07	9.14	5000
Cherkasskaja	50.50	40.00	5000
Karachevka	50.00	36.10	5000
Kisilivka mountain	50.41	30.51	5000
Narva	59.50	29.40	5000

Parutino	47.10	32.05	5000
Rud'	47.00	28.00	5000
Sabatinovka	47.40	30.00	5000
Sagvardzhile	41.80	42.50	5000
Sarajbulakhskij, Urtskij khrebet	40.31	44.42	5000
Sarkel castle (Belaja Vezha)	48.00	41.00	5000
Selitrjanaja cave, Razvalka mnt	43.90	42.72	5000
Sevan lake	40.30	45.18	5000
Skok	47.10	28.10	5000
Talyng-Leget	42.45	43.95	5000
Usatove	46.50	30.80	5000
Velica Pecina g	46.29	16.04	5000
Veternica cave d	45.84	15.87	5000
Vishgorod	50.50	30.50	5000
Cheremukhovo 1 (stratum 5)	60.24	60.03	4930
Okladnikov cave	67.00	33.00	3600

APPENDIX C1 – TRAIT VALUES FOR THE 54 SPECIES INCLUDED IN THE ANALYSES. BODY SIZE (W) AND DURATION HAVE BEEN LOG-TRANSFORMED.

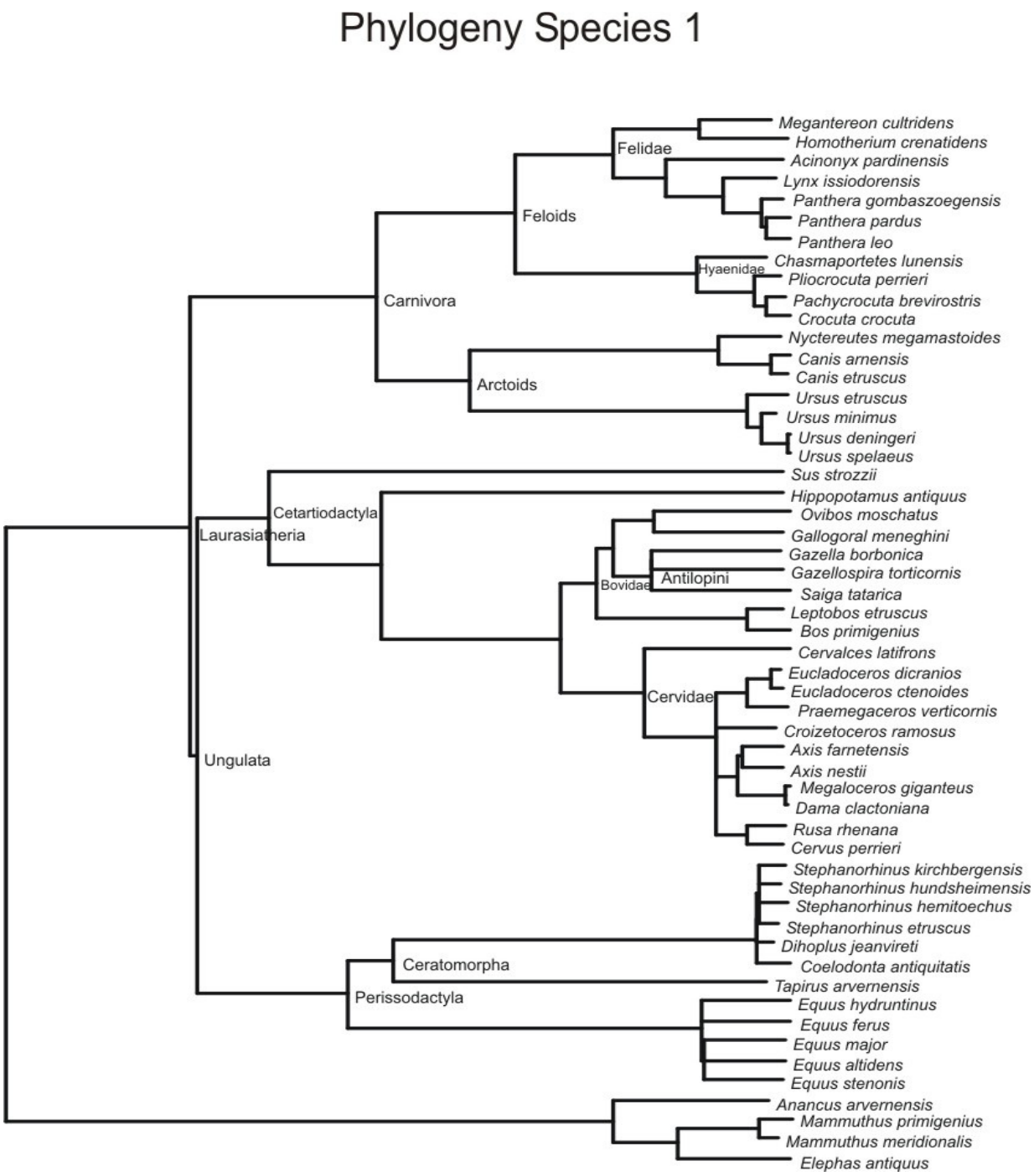
Species Name	Log W	Log Duration	Occ1	Mean Occ	Max Occ	Area 1	Mean Area	Max Area	Lat CF	Long CF
Acinonyx pardinensis	4.818	6.514	0.074	0.1	0.18	0.098	0.098	0.098	44.9	8.03
Anancus arvernensis	6.544	6.266	0.889	0.91	1	0.703	0.86	1	47.25	18.9
Axis farnetensis	4.944	5.954	0.25	0.29	0.5	0.016	0.02	0.023	43.22	11.85
Axis nestii	5.057	5.84	0.13	0.37	0.6	0.167	0.102	0.167	43.53	11.58
Bos primigenius	5.973	5.574	0.333	0.38	0.48	0.164	0.469	0.724	45.27	11
Canis arnensis	4.204	6.198	0.269	0.18	0.27	0.148	0.068	0.147	41.73	13.2
Canis etruscus	4.322	6.042	0.167	0.4	0.57	0.332	0.318	0.691	43.53	11.58
Cervalces latifrons	5.615	5.912	0.333	0.43	0.6	1	0.566	1	49.82	9.95
Cervus perrieri	5.223	6.239	0.25	0.33	0.6	0.019	0.135	0.342	44.71	23.48
Chasmaportetes lunensis	4.881	6.342	0.095	0.15	0.23	0.159	0.081	0.159	45.17	4.82
Coelodonta antiquitatis	6.462	5.42	0.118	0.23	0.3	0.623	0.687	0.752	48.82	10.45
Crocuta crocuta	5.009	5.956	0.4	0.38	0.42	0.952	0.732	0.952	47.5	8.37
Croizetoceros ramosus	4.672	6.268	0.208	0.39	0.55	0.393	0.259	0.393	45.11	3.83
Dama clactoniana	5.041	5.491	0.069	0.15	0.33	0.041	0.105	0.168	43.7	7.3
Dihoplus jeanvireti	6.358	6.181	0.546	0.57	0.67	1	0.719	1	44.71	23.16
Elephas antiquus	6.813	5.69	0.267	0.33	0.47	0.015	0.315	0.671	44	10.16
Equus altidens	5.726	5.973	0.267	0.41	0.71	0.329	0.233	0.396	44.2	10.62
Equus ferus	5.751	5.842	0.333	0.55	0.76	0.476	0.735	0.987	46.38	5.43
Equus hydruntinus	5.322	5.555	0.438	0.23	0.44	0.794	0.639	0.794	45.73	13.67
Equus major	5.914	6.465	0.118	0.19	0.27	0.512	0.356	0.512	48.31	9.3
Equus stenonis	5.612	6.172	0.2	0.54	0.81	0.81	0.599	0.81	43.53	11.58
Eucladoceros ctenoides	5.403	6.176	0.182	0.34	0.68	0.891	0.593	0.891	45.17	4.82
Eucladoceros dicranios	5.403	5.854	0.25	0.36	0.55	0.09	0.039	0.089	43.53	11.58
Gallogoral meneghini	5.217	5.776	0.333	0.29	0.38	0.034	0.218	0.403	45.17	4.82
Gazella borbonica	4.38	6.024	0.4	0.41	0.5	0.042	0.136	0.27	45.11	3.83
Gazellospira torticornis	5.459	6.111	0.25	0.32	0.5	0.153	0.274	0.396	45.11	3.83
Hippopotamus antiquus	6.473	6.075	0.35	0.47	0.75	0.182	0.443	1	43.2	11.53
Homotherium crenatidens	5.364	6.43	0.091	0.27	0.41	0.655	0.504	0.655	45.17	4.82
Leptobos etruscus	5.602	5.779	0.214	0.45	0.71	0.049	0.098	0.174	43.61	11.45
Lynx issiodorensis	4.342	6.466	0.235	0.23	0.29	0.617	0.219	0.617	43.62	11.47
Mammuthus meridionalis	6.796	6.299	0.6	0.68	0.79	0.511	0.772	1	43.62	11.47
Mammuthus primigenius	6.632	5.84	0.053	0.22	0.35	0.593	0.662	0.731	48.55	10.15
Megaloceros giganteus	5.589	5.552	0.25	0.41	0.71	0.635	0.63	0.76	48.4	9.77
Megantereon cultridens	4.799	5.979	0.167	0.22	0.32	0.016	0.132	0.334	45.13	3.45
Nyctereutes megamastoides	3.845	6.099	0.222	0.36	0.5	0.234	0.251	0.268	45.11	3.83
Ovibos moschatus	5.566	5.371	0.143	0.07	0.14	0.047	0.11	0.174	48.55	10.15
Pachycrocuta brevirostris	5.104	6.102	0.5	0.34	0.5	0.597	0.41	0.597	43.53	11.58
Panthera gombaszoegensis	4.954	6.179	0.24	0.18	0.24	0.379	0.25	0.379	42.98	12.25
Panthera leo	5.262	5.642	0.192	0.39	0.57	0.249	0.761	0.997	48.77	11.05

Panthera pardus	4.778	5.694	0.143	0.17	0.24	0.031	0.242	0.384	45.31	10.59
Pliocrocuta perrieri	4.881	6.292	0.143	0.33	0.45	0.173	0.277	0.501	45.17	4.82
Praemegaceros verticornis	5.328	6.005	0.167	0.27	0.58	1	0.505	1	49.16	8.3
Rusa rhenana	4.851	6.409	0.286	0.33	0.5	0.012	0.288	0.535	45.17	4.82
Saiga tatarica	4.462	5.555	0.097	0.1	0.1	0	0.254	0.605	45.25	33.87
Stephanorhinus etruscus	6.129	6.37	0.714	0.51	0.71	0.421	0.348	0.67	44.55	10.42
Stephanorhinus hemitoechus	6.341	5.555	0.32	0.29	0.43	0.239	0.266	0.481	45.04	5.07
Stephanorhinus hundsheimensis	6.186	6.078	0.692	0.31	0.69	0.461	0.319	0.461	42.98	12.25
Stephanorhinus kirchbergensis	6.452	5.614	0.182	0.29	0.56	0.399	0.518	0.915	49.5	11.55
Sus strozzii	5.425	5.958	0.227	0.47	0.67	0.583	0.331	0.583	43.53	11.58
Tapirus arvernensis	5.185	6.156	0.714	0.57	0.71	0.307	0.37	0.662	46.11	25.53
Ursus deningeri	5.439	5.745	0.333	0.3	0.59	0.732	0.394	0.732	49.33	8.81
Ursus etruscus	5.204	6.304	0.115	0.32	0.48	0.105	0.304	0.554	43.62	11.47
Ursus minimus	5.017	6.213	0.5	0.35	0.5	0.668	0.422	0.667	43.4	12.8
Ursus spelaeus	5.439	5.538	0.103	0.38	0.71	0.022	0.362	0.604	45.73	13.67

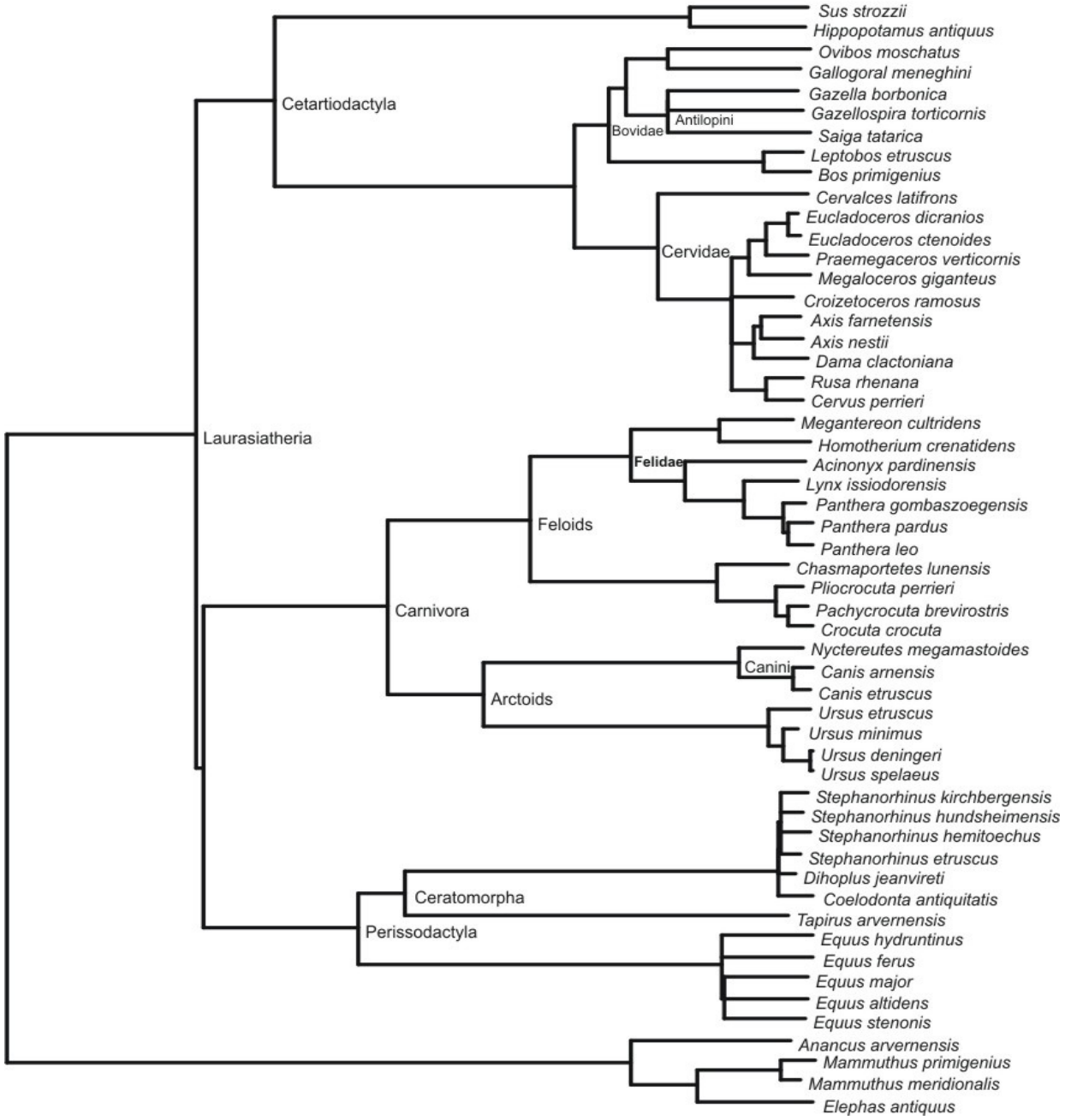
APPENDIX C2 - TRAIT VALUES FOR THE 20 GENERA INCLUDED IN THE ANALYSES. BODY SIZE (W) AND DURATION HAVE BEEN LOG-TRANSFORMED.

Genus	Log W	Log Duration	Occ1	Mean Occ	Max Occ	Area1	Mean Area	Max Area	Lat CF	Long CF
Axis	4.959	6.493	0.067	0.292	0.417	0.668	0.348	0.668	43.22	11.85
Bison	5.817	6.070	0.417	0.385	0.444	0.562	0.475	0.861	48.82	10.45
Canis	4.267	6.285	0.250	0.345	0.621	0.461	0.228	0.461	42.87	12.38
Cervalces	5.615	6.242	0.200	0.263	0.500	0.106	0.079	0.106	49.33	8.81
Equus	5.681	6.531	0.211	0.614	0.841	0.113	0.764	1.000	45.30	10.59
Eucladoceros	5.403	6.235	0.273	0.488	0.759	0.174	0.432	0.888	43.61	11.45
Gazella	5.055	6.483	0.364	0.271	0.444	0.545	0.320	0.545	45.11	3.80
Hemitragus	5.193	6.265	0.059	0.060	0.074	0.228	0.130	0.228	43.00	2.95
Hippopotamus	6.437	6.154	0.364	0.502	0.909	0.315	0.395	1.000	44.00	11.25
Homotherium	5.403	6.520	0.136	0.287	0.389	0.285	0.319	0.367	44.90	8.03
Leptobos	5.424	6.456	0.136	0.327	0.489	0.024	0.125	0.204	43.61	11.45
Mammuthus	6.780	6.472	0.500	0.619	0.829	0.665	0.865	1.000	48.55	10.17
Megaloceros	5.498	6.006	0.214	0.245	0.270	0.240	0.497	0.678	48.37	9.72
Megantereon	4.771	6.126	0.235	0.260	0.333	0.121	0.150	0.392	45.11	3.80
Ovibos	5.566	5.371	0.286	0.123	0.286	0.047	0.212	0.377	49.43	17.44
Panthera	5.045	6.273	0.261	0.276	0.366	0.379	0.484	0.963	45.65	11.20
Praemegaceros	5.397	6.270	0.074	0.256	0.500	0.226	0.344	0.744	44.35	11.70
Stephanorhinus	6.296	6.529	0.150	0.462	0.743	0.025	0.469	0.884	44.55	10.42
Sus	5.279	6.418	0.417	0.344	0.429	0.475	0.448	0.578	43.53	11.58
Ursus	5.308	6.558	0.455	0.391	0.455	0.901	0.600	0.660	45.65	11.20

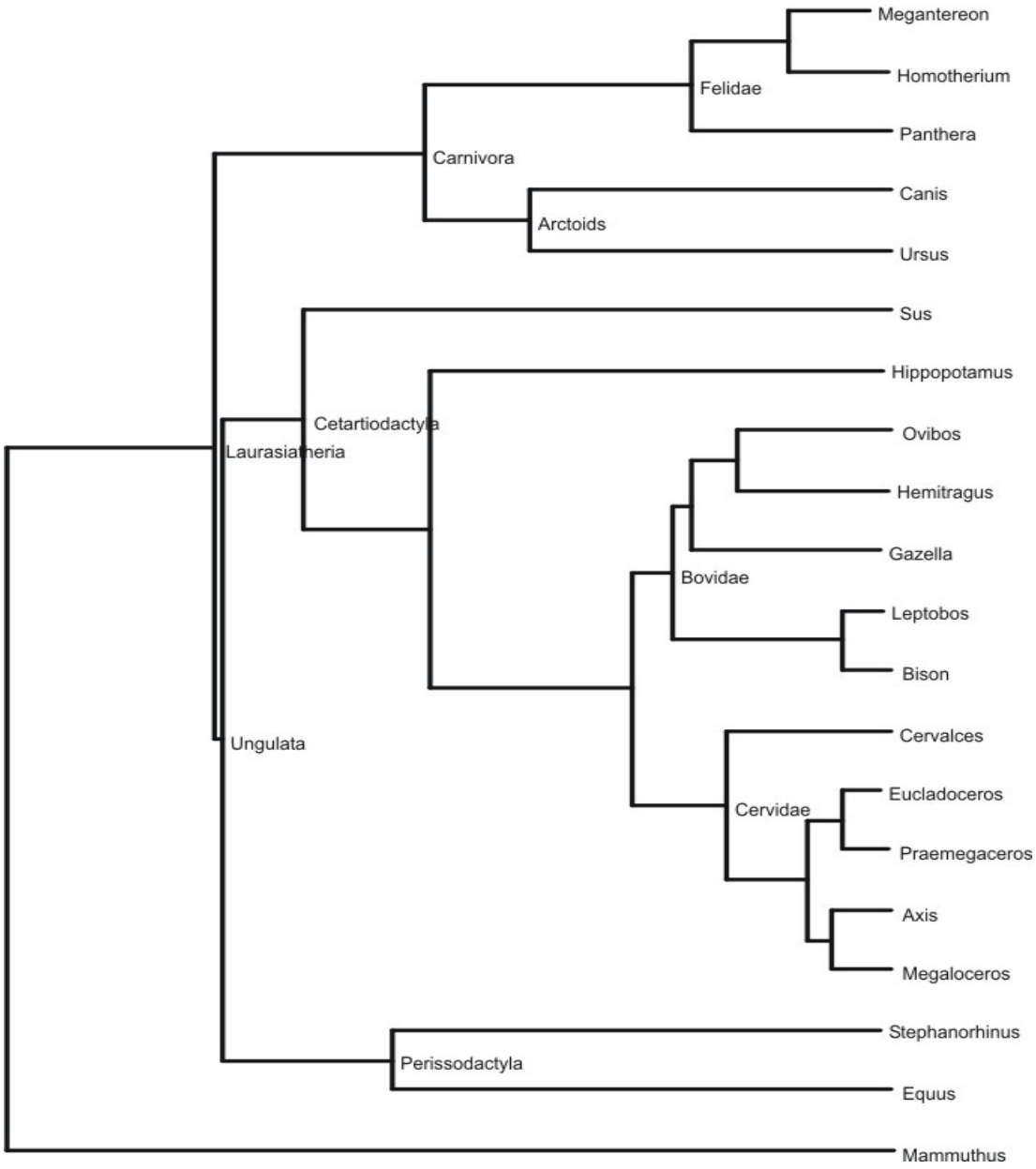
APPENDIX D – PHYLOGENIES USED FOR THE COMPARATIVE METHODS. BRANCH LENGTHS ARE PROPORTIONAL TO REAL VALUES.



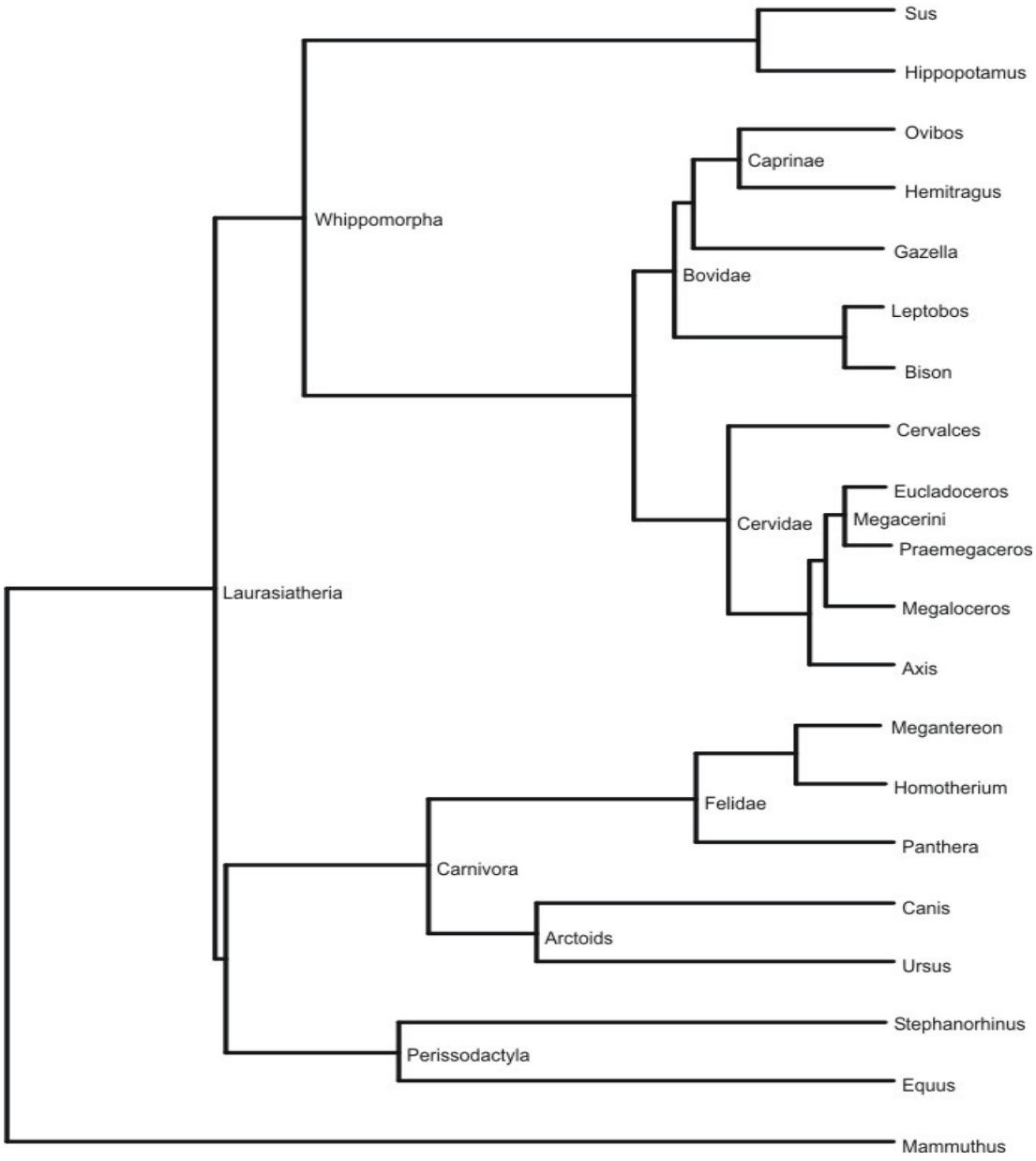
Phylogeny Species 2



Phylogeny Genera 1



Phylogeny Genera 2



LITERATURE CITED

- Ackerly, D.D. 2000. Taxon sampling, correlated evolution, and independent contrasts. Evolution 54:1480-1492.
- Adler, P.B., W.K. Lauenroth. 2003. The power of time: spatiotemporal scaling of species diversity. Ecology Letters 6:749-756.
- Adler, P.B., E.P. White, W.K. Lauenroth, D.M. Kaufman, A. Rassweiler, A.J. Rusak. 2005. Evidence for a general species-time-area relationship. Ecology 86:2032-2039.
- Alberdi, M.T., B. Azanza, E. Cerdeño, J.L, Prado. 1997. Similarity relationship between mammal faunas and biochronology from latest Miocene to Pleistocene in the Western Mediterranean area. Eclogae Geologicae Helvetiae 90:115–132.
- Alberdi, M.T., E. Ortiz-Jaureguizar, J.L. Prado. 1998. Patterns of body size changes in fossil and living Equini (Perissodactyla). Biological Journal of the Linnean Society 54:349 – 370.
- Alberdi, M.T., J.L. Prado, E. Ortiz-Jareguizar. 1995. Patterns of body size changes in fossil and living Equini (Perissodactyla). Biological Journal of Linnean Society 54:349–370.
- Alroy, J. 1992. Conjunction among taxonomic distributions and the Miocene mammalian biochronology of the Great Plains. Paleobiology 18:326–343.
- Alroy, J. 1994. Appearance event ordination: a new biochronologic method. Paleobiology 20:191–207.
- Alroy, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. Palaeogeography Palaeoclimatology Palaeoecology 127:285–311.
- Alroy, J. 1998a. Diachrony of mammalian appearance events: implications for biochronology. Geology 26:23–26.
- Alroy, J. 1998b. Cope's Rule and the Dynamics of Body Mass Evolution in North American Fossil Mammals. Science 280 (5364):731 – 734.
- Alroy, J. 1998c. Diachrony of mammalian appearance events: implications for biochronology—Reply. Geology 26:956–958.

- Alroy, J. 1998d. Equilibrial diversity dynamics in North American mammals. Pp. 232–287 *in* M.L. McKinney, J. Drake, eds. Biodiversity dynamics: turnover of populations, taxa and communities. Columbia University Press, New York.
- Alroy, J. 2000. New methods for quantifying macroevolutionary patterns and processes. Paleobiology 26:707-733.
- Anderson, S. 1984. Geographic range of North American terrestrial birds. American Museum Novitates.
- Andrews, R.M., F.H. Pough. 1985. Metabolism of squamate reptiles: Allometric and ecological relationships. Physiol. Zool. 58:214-231.
- Arnold, S.J. 1972. Species densities of predators and their prey. The American Naturalist 106:220–236.
- Arrhenius, O. 1921. Species and area. Journal of Ecology 9:95–99.
- Atkins, J.E., E.G. Boman, B. Hendrickson. 1999. A spectral algorithm for seriation and the consecutive ones problem. SIAM Journal on Computing 28:297–310.
- Azzaroli, A. 1983. Quaternary mammals and the “end-Villafranchian” event. A turning point in the history of Eurasia. Palaeogeography Palaeoclimatology Palaeoecology 44:117–139.
- Azzaroli, A., C. De Giuli, G. Ficcarelli, D. Torre. 1988. Late Pliocene to Early Mid-Pleistocene mammals in Eurasia: Faunal succession and dispersal events. Palaeogeography Palaeoclimatology Palaeoecology 66:77-100.
- Bandy, O.L. 1963a. Cenozoic planktonic foraminiferal zonation and basinal development in the Philippines. American Association of Petroleum Geologist Bullettin 47(9):1733-1745.
- Bandy, O.L. 1963b. Cenozoic planktonic foraminiferal zonation and basinal development in the Philippines (Abstract). American Association of Petroleum Geologist Bullettin 47(2):1768.
- Bandy, O.L. 1964. Cenozoic planktonic foraminiferal zonation. Micropaleontology 10(1):1-17.
- Barnosky, A.D. 2001. Distinguishing the effects of the Red Queen and Court Jester on Meiocene mammal evolution in the northern Rocky Mountains. J Vert Paleont 21:172-185.

- Barnosky, A.D., B.P. Kraatz. 2007. The role of climatic change in the evolution of mammals. Bioscience 57:523-532.
- Barnosky, A.D., E.A Hadly, C.J. Bell, 2003. Mammalian response to global warming on varied temporal scales. J. Mammal. 84:354– 368.
- Barnosky, A.D., M.A. Carrasco, E.B. Davis. 2005. The impact of the species-area relationship on estimates of paleodiversity. PLOS Biology 3 (266):1-5.
- Barraclough, T.G., and A.P. Vogler. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. The American Naturalist 155:419–434.
- Bellamy, P.E., S.A. Hinsley, I. Newton. 1996. Factors influencing bird species numbers in small woods in south-east England. Journal of Applied Ecology 33:249 -262.
- Bergmann, C. 1847. Über dies Verhältnisse der Wärmeökonomie der Tiere zu ihrer Größe. Gottlinger Studien 3:595-708.
- Bernor, R.L., V. Fahlbusch, H.V. Mittmann, eds. 1992. The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York.
- Beyer, H.L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.
- Bininda-Emonds, O.R.P., J.L. Gittleman, A. Purvis. 1999. Building large trees by combining phylogenetic information : a complete phylogeny of the extant Carnivora (Mammalia). Biological Reviews 74:143–175.
- Bininda-Emonds, O.R.P., M. Cardillo, K.E. Jones, R.D.E. MacPhee, R.M.D. Beck, R. Grenyer, S.A. Price, R.A. Vos, J.L. Gittleman, A. Purvis. 2007. The delayed rise of present-day mammals. Nature 446:507 – 512.
- Blackburn, T.M., K.J. Gaston. 1994. Animal body size distributions: patterns, mechanisms and implications. Trends in Ecology and Evolution 9:471-474.
- Blackburn, T.M., K.J. Gaston. 1996. Spatial patterns in geographic range sizes of bird species in the New World. Philosophical Transactions of the Royal Society, London, B 351:897-912.
- Blackburn, T.M., K.J. Gaston. 2003. Macroecology: concepts and consequences. Blackwell Science, Oxford.

- Blackburn, T.M., K.E. Jones, P. Cassey, N. Losin. 2004. The influence of spatial resolution on macroecological patterns of range size variation: a case study using parrots (Aves: Psittaciformes) of the world. Journal of Biogeography 31:285–293.
- Blomberg, S.P., T.Jr. Garland. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. J. Evol. Biol. 15:899–910.
- Blomberg, S.P., T. Garland, A.R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioural traits are more labile. Evolution 47:717–745.
- Bobe, R., A. K. Behrensmeyer. 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus Homo. Palaeogeog Palaeoclimatol Palaeoecol 207:399-420
- Bocherens, H., M. Fizet, A. Mariotti. 1994. Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. Paleogeography, Paleoclimatology, Paleoecology 107:213–225.
- Boecklen, W.J. 1986. Effects of the habitat heterogeneity on the species-area relationships of forest birds. Journal of Biogeography 13:59-68.
- Booth, K.S., G.S. Lueker. 1976. Testing for the consecutive ones property, interval graphs and graph planarity using PQ-tree algorithms, Journal of Computer and Systems Sciences 13:335-379.
- Bostrom, U. S.G. NIlsson. 1983. Latitudinal gradients and local variations in species richness and structure of birds communities on raised peat-bogs in Sweden. Ornis Scandinavica 14:213-226.
- Bowen, G.J., W.C. Clyde, P.L. Koch, S. Ting, J. Alroy, T. Tsubamoto, Y. Wang. 2002. Mammalian Dispersal at the Paleocene/Eocene Boundary. Science 15 (295):2062 – 2065.
- Brashares, J. S. 2003. Ecological, behavioral, and life-history correlates of mammal extinctions in West Africa. Conservation Biology 17:733–743.
- Brett, C.E., G. C. Baird. 1995. Coordinated stasis and evolutionary ecology of Silurian to middle Devonian faunas in the Appalachian basin. Pp. 285-315 *in* Erwin, D.H., R.L. Anstey, eds. New Approaches to Speciation in the Fossil Record Columbia University Press, New York, N.Y.
- Brodkorb, P. 1958. Fossil birds from Idaho. Wilson Bulletin 70:237-242.

- Brody, S. 1945. Bioenergetics and Growth. Reinhold Publishing Corporation, New York.
- Brown, J.H. 1984. On the relationship between abundance and distribution of species. The American Naturalist 124:255-79.
- Brown, J.H. 1995. Macroecology, University of Chicago Press, Chicago.
- Brown, J.H, B.A. Maurer. 1987b. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. The American Naturalist 130:1-17.
- Brown, J.H., P.F. Nicoletto. 1991. Spatial scaling of the species composition - body masses of North-American land mammals. The American Naturalist 138(6):1478-1512.
- Brown, J.H., G.B. West. 2000. Scaling in Biology. Oxford University Press. 352pp.
- Brugal, J.P., R. Croitor R. 2004. New insights concerning Lower Pleistocene cervids and bovids in Europe: dispersal and correlation. 18th International Senckenberg Conference, VI International Palaeontological Colloquium in Weimar: Late Neogene and Quaternary biodiversity and evolution : regional developments and interregional correlations, Weimar. Conference Volume. L. C. Maul and **R**.-D. Kahlke: 84-85.
- Buckley, R.C. 1982. The habitat-unit model of island biogeography. Journal of Biogeography 9:339-344.
- Bullock, J.M., I.M. Moy, R.E. Pywell, S.J. Coulson, A.M. Nolan, H. Caswell. 2002. Plant dispersal and colonization processes at local and landscape scales. pp. 279-302 in Bullock, J.M., R. Kenward, R. Hails. Dispersal Ecology. Blackwell Science, Oxford.
- Bunge, J. M. Fitzpatrick. 1993, Estimating the number of species: a review. J. Amer. Stat. Assoc. 88:364–373.
- Burnett, M.R., P.V. August, J.H. Jr. Brown, K.T. Killingbeck. 1988. The influence of geomorphological heterogeneity on biodiversity. I. A. patch-scale perspective. Conservation Biology 12:363-370.
- Butler, M.A., A.A King. 2004. Phylogenetic comparative analysis: A modeling approach for adaptive evolution. The American Naturalist 164(6):683-695.

- Calder W.A. 1996. Size, function and life history. Pp 431, Dover Publications. Mineola, New York.
- Caloi, L., M.R. Palombo, 1998. Rapporti tra carnivori ed erbivori prede e predatori nel Pliocene medio-Pleistocene medio nella penisola italiana. Geologica Romana 34:115–130.
- Cao, Y., M. Fujiwara, M. Nikaido, N. Okada, M. Hasegawa. 2000. Interordinal relationships and timescale of eutherian evolution as inferred from mitochondrial genome data. Gene 259:149–158.
- Carbone, C., G.M. Mace, C.S. Roberts, D.W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402:286–288.
- Cardillo, M., L. Bromham. 2001. Body size and risk of extinction in Australian mammals. Conservation Biology 15:1435-1440.
- Cardillo M., J.S. Huxtable, L. Bromham. 2003. Geographic range size, life history and rates of diversification in Australian mammals. Journal of Evolutionary Biology 16:282-8.
- Cavalli-Sforza, L.L., A.W.F. Edwards. 1967. Phylogenetic analysis: Models and estimation procedures. Evolution 21:550–570.
- Cerdeño, E. 1995. Cladistic Analysis of the Family Rhinocerotidae (Perissodactyla). American Museum Novitates 3143:1-25.
- Cheverud, J. 1985. A quantitative genetic model of altruistic selection. Behavioral Ecology and Sociobiology 16:239-243.
- Chown, S.L., K.J. Gaston. 1997. The species-body size distribution: energy, fitness and optimality. Functional Ecology 11:365–375.
- Christiansen, P. 1999. What size were *Arctodus simus* and *Ursus spelaeus* (Carnivora: Ursidae)? Annales Zoologici Fennici 36:93–102.
- Christiansen, P. 2004. Body size in proboscideans, with notes on elephant metabolism. Zoological Journal of the Linnean Society 140:523–549.
- Chung, F.R.K., 1997. Spectral graph theory. CBMS Regional Conference Series in Mathematics 92. American Mathematical Society, Providence, R.I.
- Cohen, J.E. 1977. Ratio of prey to predators in community food webs. Nature 270:165–167.

- Collins, S.L., S.M. Glenn. 1997. Effects of organismal and distance scaling on analysis of species distribution and abundance. Ecological Applications 7:543-551.
- Connor, E. F., E. D. McCoy. 1979. The statistics and biology of the species-area relationship. Am Nat 113: 791-833.
- Cowlay, M.J.R., C.D. Thomas, J.A. Thomas, M.S. Warren. 1999. Flight areas of British butterflies: assessing species status and decline. Proceedings of The Royal Society, London B 266:1587-1592.
- Croft, D. 2006. Do marsupials make good predators? Insights from predator–prey diversity ratios. Evolutionary Ecology Research 8 (7):1193–1214.
- Croitor, R. 2004. Systematics and phylogeny of large-sized deer of the genus *Praemegaceros* Portis, 1920 (Cervidae, Mammalia). 18th International Senckenberg Conference in Weimar. Abstract Book.
- Damuth, J., 1982. Analysis of the preservation of community structure in assemblages of fossil mammals. Paleobiology 8:434-446.
- Damuth, J., B.J. MacFadden. 1990. Body Size in Mammalian Paleobiology. Cambridge Univ. Press.
- Dawson, T.J. A.J. Hulbert. 1970. Standard metabolism, body temperature and surface areas of Australian marsupials. Am. J. Physiol. 218:1233-1238.
- Dayan, T., D. Simberloff. 2005. Ecological and community-wide character displacement: the next generation. Ecology Letters 8: 875-894.
- Domingo M.S., M.T. Alberdi, B. Avanza. 2007. A new quantitative biochronological ordination for the Upper Neogene mammalian localities of Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 255:361-376.
- Dony, J.G. 1970. Species-Area Relationship. Unpublished Report to the Natural Environment Research Council.
- Efron, B. 1979. Bootstrap Methods: Another Look at the Jackknife. The Annals of Statistics 7(1):1–26.
- Efron, B., R.J. Tibshirani. 1993. An Introduction to the Bootstrap, London, Chapman & Hall.
- Felsenstein, J. 1985. Phylogenies and the comparative method. The American Naturalist 125:1–15.

- Felsenstein, J. 1988. Phylogenies and quantitative characters. Annu. Rev. Ecol. Syst. 19:445–471.
- Felsenstein, J. 2004. Inferring phylogenies. Sinauer, Sunderland, Massachusetts.
- Fiedler, M. 1975. Eigenvectors of acyclic matrices. Czechoslovak Mathematical Journal 25(4):607–618.
- Finarelli, J.A., and J.J. Flynn. 2006. Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): the effects of incorporating data from the fossil record. Systematic Biology 55:301–313.
- Fisher, R.A., A.S. Corbet, C.B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology 12:42-58.
- Flebbe, P.A. 1994. A regional view of the margin: salmonid abundance and distribution in the southern Appalachian mountains of North Carolina and Virginia. Transactions of the American Fisheries Society 123:657-667.
- Foote, M. 2007. Symmetric waxing and waning of marine animal genera. Paleobiology 33:517-529.
- Foote, M., J.S. Crampton, A.G. Beu, B.A. Marshall, R.A. Cooper, I. Matcham. 2007. Rise and fall of species occupancy in Cenozoic marine molluscs. Science 318:1131-1134.
- Foote, M., J.S. Crampton, A.G. Beu, R.A. Cooper. 2008. On the bidirectional relationship between geographic range and taxonomic duration. Paleobiology 34:421-433.
- Ford, H.A. 1987. Bird communities in habitat islands in England. Bird Study 34:205-218.
- Fortelius M., A. Gionis, J. Jernvall, H. Mannila. 2006. Spectral ordering and biochronology of European fossil mammals. Paleobiology 32(2): 206-214.
- Fortelius, M., L. Werdelin, P. Andrews, R. L. Bernor, A. Gentry, L. Humphrey, W. Mittmann, S. Viranta. 1996. Provinciality, diversity, turnover and paleoecology in land mammal faunas of the later Miocene of western Eurasia. Pp. 414-448 *in* Bernor, R.L., V. Fahlbusch, W. Mittmann eds. The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press.

- Fox, B.J. 1983. Mammal species diversity in Australian heathlands: the importance of pyric succession and habitat diversity. Pp. 473-489 *in*: Kruger, F.J., D.T. Mitchell, J.U.M. Jarvis eds. Mediterranean-Type Ecosystems: The Role of Nutrients. Springer-Verlag, Berlin.
- Freckleton, R.P., J.A. Gill, D. Noble, A.R. Watkinson. 2005. Large-scale population dynamics, abundance-occupancy relationships and the scaling from local to regional population size. Journal of Animal Ecology 74:353-364.
- Freckleton, R.P., P.H. Harvey, M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. The American Naturalist 160:712–726.
- Freckleton, R.P., A.R. Watkinson, R.E. Green, W.J. Sutherland. 2006. Census error and the detection of density-dependence. Journal of Animal Ecology 75:837–851.
- Garland, T.Jr., A.F. Bennett, E.L. Rezende. 2005. Phylogenetic approaches in comparative physiology. Journal of Experimental Biology 208:3015-3035.
- Garland, T.Jr., A.W. Dickerman, C.M. Janis, J.A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Syst. Biol. 42:265-292.
- Garland, T.Jr., R. Díaz-Uriarte. 1999. Polytomies and phylogenetically independent contrasts: examination of the bounded degrees of freedom approach. Syst. Biol. 48:547-558.
- Garland, T.Jr., P.E. Midford, A.R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. Am. Zool. 39:374-388.
- Gaston, K.J. 1991a. Body size and probability of description: the beetle fauna of Britain. Ecological Entomology 16:505-508.
- Gaston, K.J. 1991b. The magnitude of global insect species richness. Conservation Biology 5:283-296.
- Gaston, K.J. 1991c. How large is a species' geographic range? Oikos 61:434-437
- Gaston, K.J. 1994. Measuring geographic range size. Ecography 17:198-205.

- Gaston, K.J. 1998. Species-range size distributions: products of specieation, extinction and transformation. Philosophical Transactions of the Royal Society, London, B 353:219-230.
- Gaston, K.J. 2003. The structure and dynamics of geographic range. *In* Ecology and Evolution. Oxford University Press, Oxford.
- Gaston, K.J., T.M. Blackburn, J. Lawton, 1997. Interspecific abundance-range size relationships: an appraisal of mechanisms. J Animal Ecology 66:579-601.
- Gaston, K.J., T.M. Blackburn, R.D. Gregory. 1999a. Intraspecific abundance-range size relationships: case studies of six bird species in Britain. Diversity and Distributions 5:197-212.
- Gaston, K.J., T.M. Blackburn, R.D. Gregory. 1999b. Does variations in census area confound density compensations? Journal of Applied Ecology 36:191-204.
- Gaston, K.J., T.M. Blackburn. 2000. Pattern and process in macroecology. Blackwell Science, Oxford.
- Gaston, K.J., P.H. Warren, P. M. Hammond. 1992. Predator: non-predator ratios in beetle assemblages. Oecologia 90:417–421.
- Geisler, J.H., M.D. Uhen. 2005. Phylogenetic Relationships of Extinct Cetartiodactyls: Results of Simultaneous Analyses of Molecular, Morphological, and Stratigraphic Data. Journal of Mammalian Evolution 12:145-169.
- Geraads, D.1992. Phylogenetic analysis of the tribe Bovini (Mammalia: Artiodactyla). Zoological Journal of the Linnean Society 104:193–207.
- Gittleman, J.L. 1985. Carnivore body size: ecological and taxonomic correlates. Oecologia 67:540–554.
- Gleason, H.A. On the relation between species and area. Ecology 6:66-74.
- Gliozzi, E., L. Abbazzi, P. Argenti, A. Azzaroli, L. Caloi, L. Capasso Barbato, G. Di Stefano, D. Esu, G. Ficcarelli, O. Girotti, T. Kotsakis, F. Masini, P. Mazza, c. Mezzabotta, M. R. Palombo, C. Petronio, L. Rook, B. Sala, R. Sardella, E. Zanalda, D. Torre, 1997. Biochronology of selected mammals, molluscs and ostracods from the middle Pliocene to the late Pleistocene in Italy. The state of the art. Rivista Italiana di Paleontologia e Stratigrafia 103:369–388.
- Godall, D.W. 1952. Quantitative aspects of plant distribution. Biological Reviews 27:194-245.

- Gotelli, N.J., R.K. Colwell. 2001. Quantigying biodiversity: procedures and pitfalls in the measurement and comparison of spcies richness. Ecology Letters 4 (4):379-391.
- Gotelli, N.J., D. Simberloff. 1987. The distribution and abundance of tallgrassprairie plants: a test of the core-satellite hypothesis. The American Naturalist 130:18–35.
- Grafen, A. 1989. The phylogenetic regression. Phil. Trans. R. Soc. Lond. B 326:119-157.
- Grantham, T.A. 1995. Hierarchical approaches to macroevolution: recent work on species selection and the "effect hypothesis." Annual Review of Ecology and Systematics 26:301–322.
- Grinnel, J. 1922. The role of the "accidental". Auk 39:373-380.
- Hadly, E. A., B. A. Maurer. 2001. Spatial and temporal patterns of species diversity in montane mammal communities of western North America. Evol Ecol Res 3:477-486.
- Haila, Y., O. Järvinen. 1983. Land birds communities on a Finish island: species impoverishment and abundance patterns. Oikos 41:255–273.
- Hair J.F., B. Black, B. Babin, R.E. Anderson, R.L. Tatham. 2001. Multivariate Data Analysis. Prentice Hall.
- Hammer, Ø., D.A.T. Harper, P.D. Ryan. 2001, PAST: Paleontological statistical package for education and data analysis. Paleontologia Electronica 4, 9pp. Version 1.42.
- Hanski, I. 1982a. Dynamics of regional distribution: the core and satellite speices hypothesis. Oikos 38:210-221.
- Hanski, I. 1982b. Distributional ecology of anthropochorous in villages surrounded by forest. Annales Botanici Fennici 19:1-15.
- Hanski, I. 1982d. On patterns of temporal and spatial variation in animal populations. Annales Zoologici Fennici 19:21–37.
- Hanski, I. 2000. Extinction debt and species credit in boreal forests: modelling the consequences of different approaces to biodiversity conservation. Ann. Zool. Fennici 37:271-280.

- Hanski, I., J. Kouki, A. Halkka. 1993. Three explanations of the positive relationship between distribution and abundance of species. Pp. 108-116 *in* Ricklefs R.E., D. Schluter, eds. Species Diversity in Ecological Communities.
- Harmon L., J. Weir, C. Brock, R. Glor, W. Challenger, G. Hunt. 2008. Geiger: Analysis of evolutionary diversification. R package version 1.2-14.
- Harner, R.F., K.T. Harper. 1976. The role of area, heterogeneity, and favorability in plant species diversity of pinyon–juniper ecosystems. Ecology, 57:1254–1263.
- Harte, J., T. M. Blackburn, and A. Ostling. 2001. Self-similarity and the relationship between abundance and range size. The American Naturalist 157:374–386.
- Harvey, P.H., M.D. Pagel. 1991. The Comparative Methods in Evolutionary Biology. Oxford University Press, Oxford.
- He, F., P. Legendre. 1996. On species-area relations. The American Naturalist 148:719-737.
- Hecnar, S.J. 1999. Patterns of turtle species' geographic range size and a test of Papoport's rule. Ecography 22:436-446.
- Hernández Fernández, M., B. Azanza, M.A. Álvarez Sierra. 2004. Iberian Plio-Pleistocene biochronology: micromammalian evidence for MNs and ELMAs calibration in southwestern Europe. Journal of Quaternary Science **19**:605–616.
- Hernández Fernández, M., E.S. Vrba. 2005. A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. Biological Reviews 80:269-302.
- Holt, R.D, J.H. Lawton, K.J. Gaston. T.M. Blackburn. 1997. On the relationship between range size and local abundance: back to basis. Oikos 78:183-190.
- http://paleodb.org/cgi-bin/bridge.pl
- http://www.helsinki.fi/science/now/
- http://www.pangaea.de
- Hunt, G., K. Roy, and D. Jablonski. 2005. Species-level heritability reaffirmed: a comment on "On the heritability of geographic range sizes." The American Naturalist 166:129–135.
- Hutchinson , G.E., R.H. MacArthur. 1959. A theoretical ecological model of size distributions among species of animals. The American Naturalist 93:117-125.

- Imbrie, J., A. Berger, N.J. Shackleton. 1993. Role of orbital forcing: a two-million year perspective. Pp. 263-267 *in* Eddy, J.A., H. Oeschger eds. Global Changes in the Perspective of the Past. John Wiley & Sons, New York.
- Jablonski, D. 1986. Background and mass extinctions: the alteration of macroevolutionary regimes. Science 231:129-133.
- Jablonski, D. 1987. Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. Science 238:360–363.
- Jablonski, D., G. Hunt. 2006. Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: Organismic vs. species-level explanations. The American Naturalist 168:556-564.
- Jablonski, D., J.W. Valentine. 1990. From regional to total geographic ranges: testing the relationship in Recent bivalves. Paleobiology 16:126-142.
- Janis, C.M. 2008. An Evolutionary History of Browsing and Grazing Ungulates. Pp 21-45 *in* I. J.Gordon, H.H.T. Prins, eds. The Ecology of Browsing and Grazing, Springer.
- Jeffries, M.J., J.H. Lawton. 1985. Predator–prey ratios in communities of freshwater invertebrates: the role of enemy free spaces. Freshwater Biology 15:105–112.
- Jenkins, D.G. 1992. Predicting extinctions of some extant planktic Foraminifera. Marine Micropaleontology 19:239–243.
- Jernvall, J., M. Fortelius. 2002. Common mammals drive the evolutionary increase of hypsodonty in the Neogene. Nature 417:538-540.
- Jernvall, J., M. Fortelius. 2004. Maintenance of trophic structure in fossil mammal communities: site occupancy and taxon resilience. The American Naturalist 164:614-624
- Johnson, C.N. 1998. Species extinction and the relationship between distribution and abundance. Nature 394:272–274.
- Johnson, R.H. 1975. Controls of number of birds species on montane islands in the Great Basin. Evolution 29:545-567.
- Jones, K.E., W. Sechrest, J.L. Gittleman. 2005. Age and area revisited: identifying global patterns and implications for conservation. Pp 141–165 *in*

Purvis A., J. L. Gittleman, T. M. Brooks, eds. Phylogeny and conservation. Cambridge University Press, Cambridge.

- Kallimanis, A. S., A. D. Mazaris, J. Tzanopoulos, J. M. Halley, J. D. Pantis, S. P. Sgardelis. 2008. How does habitat diversity affect the species-area relationship? Global Ecol Biogeog 17:532-538.
- Kelt, D.A., D. Van Vuren. 1999. On the relationship between body size and home range area: consequences of energetic constraints in mammals. Ecology 80:337-400.
- Kembel, S., D. Ackerly, S. Blomberg, P. Cowan, M. Helmus, H. Morlon, C. Webb. 2009. picante: R tools for integrating phylogenies and ecology. R package version 0.7-0.
- Kidwell, S.M. K.W. Flessa. 1996. The quality of the fossil record: Populations, species and communities. Ann. Rev. Earth Planet. Sci. 24:433-464. [Reprint, with addendum, of Kidwell and Flessa (1995)].
- Kinzig, A.P., J. Harte. 2000. Implications of endemics-area relationships for estimates of species extinctions. Ecology 81(12):3305-3311.
- Kitchener, D.J., A. Chapman, J. Dell, B.G. Muir, M. Palmer. 1980a. Lizard assemblage and reserve size and structure in the Western Australian wheatbelt some implications. Biological Conservation 17:25–62.
- Kitchener, D.J., A. Chapman, J. Dell, B.G. Muir, M. Palmer. 1980b. The conservation value of mammals of reserves in the Western Australian wheatbelt. Biological Conservation 18:179–207.
- Kleiber, M. 1932. Body size and metabolism. Hilgardia 6:315–351.
- Klein, R.G. 1986. Carnivore size and Quaternary climatic change in Southern Africa. Quaternary Research 26:153–170.
- Klein, R.G., K. Scott. 1989. Glacial/Interglacial size variation in fossil spotted hyenas (Crocuta crocuta) from Britain. Quaternary Research 32:88–95.
- Koenigswald, W. von, L. Werdelin. 1992. Mammalian Migration and dispersal events in the European quarternary. Courier Forschung-Institute 153.
- Kot, M., M.A. Lewis, P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. Ecology 77(7):2027–2042.

- Kozlowski, J., A.T. Gawelczyk. 2002. Why are species body size distributions usually skewed to the right? Functional. Ecology 16:419–432.
- Krebs, C.J. .1988. The message of ecology. Harper & Row, New York.
- Krebs, C.J. .1994. Ecology: the experimental analysis of distribution and abundance. Harper & Row, New York.
- Kuehn, R., C.J. Ludt, W. Shroeder, O. Rottmann. 2005.Molecular phylogeny of *Megaloceros giganteus*–the Giant Deer or just a Giant Red Deer? Zoological Science 22:1031–1044.
- Lacombat, F. 2006. Pleistocene rhinoceros in mediterranean Europe and in Massif Central (France). Courier Forschungsinstitut Senckenberg 256:57-69.
- Lasiewski, R.C. W.R. Dawson. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69:13-23.
- Lavin S.R., W.H. Karasov, A.R. Ives, K.M. Middleton, T.Jr. Garland. 2008. Morphometrics of the Avian Small Intestine Compared with That of Nonflying Mammals: A Phylogenetic Approach. Physiological and Biochemical Zoology 81(5):526–550.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.
- Lindsay, E. 2003. Chronostratigraphy, Biochronology, Datum Events, Land Mammal Ages, Stage of Evolution, and Appearance Event Ordination. Bullettin of American Museum Natural History 279:212-230.
- Liow, L.H., N.C. Stenseth. 2007. The rise and fall of species: implications for macroevolutionary and macroecological studies. Proceedings of the Royal Society B-Biological Sciences 274:2745–2752.
- Lister, A.M. 2004. The impact of Quaternary Ice Ages on mammalian evolution. *Philosophical Transactions of Royal Society of London* B, **359**:221-241.
- Lister, A.M., C.J. Edwards, D.A.W. Nock, M. Bunce, I. A.van Pijlen, D.G. Bradley, M.G. Thomas, I. Barnes. 2005. The phylogenetic position of the 'giant deer' *Megaloceros giganteus*. Nature 438:850-3.

- Looijen, R.C. 1995. On the distinction between habitat and niche, and some implications for species' differentiation. Poznan´ Studies in the Philosophy of the Sciences and the Humanities 45:87–108.
- Looijen, R.C. 1998. Holism and reductionism in biology and ecology. The mutual dependence of higher and lower level research programmes. PhD Thesis, University of Groningen, Groningen.
- Lynch, M. 1991. Methods for analysis of comparative data in evolutionary biology. Evolution 45:1065–1080.
- MacArthur, R.H. 1959. On the breeding distribution pattern of North American migrant-birds. Auk 76:318-325.
- MacArthur, R.H. 1972. Geographical Ecology. 269pp. Harper and Row.
- MacArthur, R.H., E. O. Wilson. 1967. The Theory of Island Biogeography. 203pp. Princeton.
- MacMillen, R.E. J.E. Nelson. 1969. Bioenergetics and body size in dasyurid marsupials. Am. J. Physiol. 217:1246-1251.
- Magurran, A. E. 2007. Species abundance distributions over time. Ecology Lett 10:347-354.
- Martins, E.P., T.F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am. Nat. 149:646-667. Erratum Am. Nat. 153:448.
- Maslin, M.A., X.S. Li, M.F. Loutre, A. Berger. 1998. The contribution of orbital forcing to the progressive intensification of Northern Hemisphere glaciation. Quaternary Science Review 17:411-426.
- Maurer, B.A. 1999. Untangling Ecological Complexity. University of Chicago Press, Chicago.
- Maurer, B.A., J.H. Brown, R.D. Rusler. 1992. The micro and macro in body size evolution. Evolution 46:939-953.
- May, R. M. 1975. Patterns of species abundance and diversity. In: Diamond ML, Cody JM (eds) Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts, USA, pp 81–120.
- Mazza, P., M. Rustioni.1994. On the phylogeny of Eurasian bears. Palaeontographica Abt. A 230:1-38.

- McCollin, D. 1993. Avian distribution patterns in a fragmented wooded landscape (North Humberside, U.K.); the role between-patch and within-patch structure. Global Ecology and Biogeography Letters 3:48-62.
- McGeogh, M.A., K.J. Gaston. 2002. Occupancy frequency distributions: patterns, artefacts and mechanisms. Biological Review 77:311-31.
- McIntosh, R.P. 1967. An index of divertity and the relation of certain concepts to diversity. Ecology 48:392-404.
- McKinney, M.L., D.L. Frederick. 1999. Species–time curves and population extremes: ecological patterns in the fossil record. Evolutionary Ecology Research 1:641–650.
- McNab, B.K. 1971. On the ecological significance of Bergmann's rule. Ecology 52:845-855.
- Mein, P. 1975. Résultats du groupe de travail des vertébrés: bizonation du Néogéne méditerranéen à partir des Mammiféres. Report Activity RCMNS working groups, Bratislava 78–81.
- Meloro, C., P. Raia, C. Barbera. 2007. Effect of predation on prey abundance and survival in Plio-Pleistocene mammalian communities. Evolutionary Ecology Research 9(3):505-525.
- Meloro, C., P. Raia, F. Carotenuto, C. Barbera. 2008. Diversity and turnover of Plio-Pleistocene large mammal fauna from the Italian Peninsula. Palaeogeography Palaeoclimatology Palaeoecology 268 (1-2):58-64
- Miller, A.I. 1997. A new look at age and area: the geographic and environmental expansion of genera during the Ordovician radiation. Paleobiology 23:410–419.
- Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.
- Nee, S., J.H. Lawton. 1996. Body size and biodiversity. Nature 380:672-673.
- Newmark, W.D. 1987. A land-bridge island perspective on mammalian extinctions in western North America Parks. Nature 325:430-432.
- O'Meara, B.C., C. Ané, M.J. Sanderson, P.C. Wainwright. 2006. Testing for different rates of continuous trait evolution using likelihood. Evolution 60:922–933.

- Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877–884.
- Palombo, M.R., B. Azanza, M.T. Alberdi. 2003. Italian mammal biochronology from latest Miocene to middle Pleistocene, a multivariate approach. Geologica Romana 36 (2000–2002):335–368.
- Peck, K.M. 1989. Tree species preferences shown by foraging birds in forest plantations in northern England. Biological Conservation 48:41-57.
- Peters, R.H. 1983. The Ecological Implication of Body Size. Cambridge University Press, Cambridge.
- Petronio, C., R. Sardella. 1999. Biochronology of the Pleistocene mammal fauna from Ponte Galeria (Rome) and remarks on the middle Galerian faunas. Rivista Italiana di Paleontologia e Stratigrafia 105:155–164.
- Pfeiffer, T. 1999. Die Stellung von *Dama* (Cervidae, Mammalia) im System plesiometacarpaler Hirsche des Pleistozans. Courier Forschungsinstitut Senckenberg 211:1–-218.
- Pillar, V.D., 1999. How sharp are classifications? Ecology 80:2508–2516.
- Pillar, V.D., 2001. MULTIV 2.1.1. Program, Porto Alegre.
- Pimm, S.L., R.A. Askins. 1995. Forest losses predict bird extinctions in eastern North America. Proc. Natl. Acad. Sci. 92:9343–9347.
- Powell, M.G., 2007. Geographic range and genus longevity of late Paleozoic brachiopods. Paleobiology 33:530-546.
- Prasad, A.B., M.W. Allard, E.D. Green. 2008. Confirming the Phylogeny of Mammals by Use of Large Comparative Sequence Data Sets. Molecular Biology Evolution 25:1795–1808.
- Preston, F.W. 1948. The commonness, and rarity, of species. Ecology 29:254-283.
- Preston, F.W. 1960. Time and space and variation of species. Ecology: 41: 611–627.
- Price, S.A., O.R.P. Bininda-Emonds, J.L. Gittleman. 2005. A complete phylogeny of the whales, dolphins and even-toed hoofed mammals (Cetartiodactyla). Biological Review 80:445–473.

- Purvis, A., C.D.L. Orme, K. Dolphin. 2003. Why are most species small-bodied? A phylogenetic view. Pp 155-173 *in* T.M. Blackburn and K.J. Gaston eds, Macroecology: concepts and consequences. Blackwell Science, Oxford.
- Pyron, M. 1999. Relationships between geographic range size, body size, local abundance, and habitat breadth in North American suckers and sunfishes. Journal of Biogeography 26:549-558.
- Qian, H., R.E. Ricklefs. 2004. Geographical distribution and ecological conservatism of disjunct genera of vascular plants in eastern Asia and eastern North America. Journal of Ecology 92:253–265.
- Quinn, S.L., J.B. Wilson, A.. Mark. 1987. The island biogeography of Lake Manapouri, New Zeland. Journal of Biogeography 14:569-581.
- Rafe, R.W, M.B. Usher, R.G. Jefferson. 1985. Birds on reserves: the influence of area and habitat on species richness. Journal of Applied Ecology 22:327-335.
- Raia, P. 2003. The evolutionary ecology of large mammals communities of Italy during the Ice Ages. Doctoral Thesis.
- Raia, P., F. Carotenuto, C. Meloro, P. Piras, C. Barbera T. Kotsakis. 2009. More than three million years of community evolution. The temporal and geographical resolution of the Plio-Pleistocene Western Eurasia mammal faunas. Palaeogeography Palaeoclimatology Palaeoecology 276:15-23.
- Raia, P., C. Meloro, C. Barbera. 2007. Inconstancy in predator/prey ratios in Quaternary large mammal communities of Italy, with an appraisal of mechanisms. Quaternary Research 67:255-263.
- Raia, P., C. Meloro, A. Loy, C. Barbera. 2006b. Species occupancy and its course in the past: macroecological patterns in extinct communities. Evolutionary Ecology Research 8:181–194.
- Raia, P., P. Piras T. Kotsakis. 2005. Turnover pulse or Red Queen? Evidence from the large mammal communities during the Plio-Pleistocene of Italy. Palaeogeography Palaeoclimatology Palaeoecology 221:293-312.
- Raia, P., P. Piras, T. Kotsakis. 2006a. Detection of Plio-Quaternary large mammal communities of Italy. An integration of fossil faunas biochronology and similarity. Quat Sci Rev 25:846-854.
- Rapoport, E.H. 1982. Areography: Geographical Strategies of Species. Pergamon, Oxford.

- Raunkiaer, C. 1934. The Life forms of plants and statistical plant geography. Clarendon Press, Oxford.
- Reed, T.M. 1981. The number of breeding landbird species on British Islands. Journal of Animal Ecology 50:613–624.
- Reed, T.M. 1983. The role of the species-area relationship in reserve choice: a British example. Biological Conservation 25:263-271.
- Reed, T.M. 1984. The number of landbird species on the Isles if Scilly. Biological Journal of the Linnean Society 21:431-437.
- Revell, L.J., L.J. Harmon, D.C. Collar. 2008. Phylogenetic signal, evolutionary process, and rate. Systematic Biology 57:591-601.
- Reynolds, P.S., R.M. Lee. 1996. Phylogenetic analysis of avian energetics: Passerines and nonpasserines do not differ. Am. Nat. 147:735-759.
- Ricklefs, R.E. 1979. Ecology. Chiron, New York.
- Ricklefs, R.E., E. Bermingham. 2002. The concept of the taxon cycle in biogeography. Global Ecology and Biogeography 11:353-361.
- Ridley, M. 1983. The Explanation of Organic Diversity: The Comparative Method and Adaptations for Mating. Clarendon, Oxford.
- Rigby, C., J.H. Lawton. 1981. Species-area relationships of arthropods on host plants: herbivores on bracken. Journal of Biogeography 8:125-133.
- Rodriguez, J., M.T. Alberdi, B. Azanza, J.L. Prado. 2004. Body size structure in north-western Mediterranean Plio-Pleistocene mammalian faunas. GlobalEcology and Biogeography 13:163–176.
- Rohlf, F.J. 2001. Comparative methods for the analysis of continuous variables: Geometric interpretations. Evolution 55:2143-2160.
- Rook, L., D. Torre. 1996. The wolf-event in western Europe and the beginning of the Late Villafranchian. Neuse Jahrbuch, Geologie unt Palantologie Mh H 8:495–501.
- Rosenzweig, M.L. 1991. Habitat selection and population interactions: the search for mechanism. The American Naturalist. 137:S5-S28.
- Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

- Rosenzweig, M.L. 1995. Species diversity in space and time. Cambridge Univ. Press.
- Rosenzweig, M.L. 1998. Preston's ergodic conjecture: the accumulation of species in space and time. In: McKinney M.L., Drake J.A. eds. Biodiversity dynamics: turnover of populations, taxa, and communities. Columbia University Press, New York, New York, USA, pp 311–348.
- Rosenzweig, M.L., E.A. Sandlin. 1997. Species diversity and latitudes: listening to area's signal. Oikos 80:172–175.
- Roy, K. 1994. Effects of the Mesozoic marine revolution on the taxonomic, morphologic, and biogeographic evolution of a group: aporrhaid gastropods during the Mesozoic. Paleobiology 20:274-296.
- Roy, K., D. Jablonski, J.W. Valentine. 1995. Thermally anomalous assemblages revisited; patterns in the extraprovincial latitudinal range shifts of Pleistocene marine molluscs. Geology 23:1071-1074.
- Roy, K., D. Jablonski, J.W. Valentine. 2001. Climate change, species range limits and body size in marine bivalves. Ecology Letters 4:366-370.
- Roy, K., D. Jablonski, J.W. Valentine. 2002. Body size and invasion success in marine bivalves. Ecology Letters 5:163-167.
- Sanford, G.M., W.I. Lutterschmidt, V.H. Hutchison. 2002. The comparative method revisited. BioScience 52:830-836.
- Sardella, R., L. Caloi, G. Di Stefano, M.R. Palombo, C. Petronio, L: Abbazzi, A. Azzaroli, G. Ficcarelli, P. Mazza, C. Mezzabotta, L. Rook, D. Torre, P. Argenti, L. Capasso Barbato, T. Kotsakis, E. Gliozzi, F. Masini, B. Sala, 1998. Mammal faunal turnover in Italy from the middle Pliocene to the Holocene. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO 60:499–511.
- Scheiner, S. M. 2003. Six types of species-area curves. Glob Ecol Biogeogr 12: 441–447.
- Sfenthourakis, S. 1996. The species-area relationship of terrestrial isopods (Isopoda; Oniscidea) from the Aegean archipelago (Greece): a comparative study. Global Ecol Biogeogr Letters 5(3):149-157.
- Shackleton, N.J., J.P. Kennett. 1975. Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: oxygen and carbon isotope analysis in

DSDP Sites 277, 279, and 281. Pp. 743-755 *in* Kennett, J.P., R.E. Houtz et al., Init. Repts. DSDP, 29: Washington (U.S. Govt. Printing Office).

- Shoenly, K., R.A. Beaver, T.A. Heumier. 1991. On the trophic relations of insects: a food-web approach. The American Naturalist 137:597–638.
- Shoshani, J., P. Tassy. 2005. Advances in proboscidean taxonomy & classification, anatomy & physiology, and ecology & behaviour. Quaternary International 126–128: 5–20.
- Simberloff, D. 1976. Trophic structure determination and equilibrium in an arthropod community. Ecology 57:395–398.
- Slater, G.J., B. Van Valkenburgh. 2008. Long in the tooth: evolution of sabertooth cat cranial shape. Paleobiology 34:403–419.
- Sommer, R.S., F.E. Zachos. 2009. Fossil evidence and phylogeography of temperate species: 'glacial refugia' and post-glacial recolonization. Journal of Biogeography 36:2013–2020.
- Spencer, M., L. Blaustein, S. Swaitz, J.E. Cohen. 1999. Species richness and the proportion of predatory animal species in temporary freshwater pools: relationships with habitat size and permanence. Ecology Letters 2:157–166.
- Springer, M.S., W.J. Murphy, E. Eizirik, S.J. O'Brien. 2005. Molecular evidence for major placental clades. Pp. 37–49 *in* K. D. Rose and J. D. Archibald eds. The rise of placental mammals: origins and relationships of major clades. John Hopkins Press.
- Stanley, S.M. 1973. An explanation for Cope's Rule: Evolution 27:1-26.
- Stenseth, N.C. 1979. Where have all the species gone? On the nature of the extinction and the Red Queen hypothesis. Oikos 33:196-227.
- Stiner, M., H. Achyuthan, G. Arsebuck, F.C. Howell, S.C. Josephson, K.E. Juell, J. Pigati, J. Quade. 1998. Reconstruing cave bear paleoecology from skeletons: a cross-disciplinary study of middle Pleistocene bears from Yarimburgaz Cave, Turkey. Paleobiology 24:74–98.
- Stirton, R.A. 1963. Time, life, and man. 2nd edition. John Wiley and Sons, New York.
- Sugihara, G., K. Shoenly, A. Trombla. 1989. Scale invariance and food web properties. Science 245:48–52.

- Swiderski, D.L. 2001. The role of phylogenies in comparative biology: an introduction to the symposium. Am. Zool. 41:485–486
- Theodor, J.M. 2004. Molecular clock divergence estimates and the fossil record of Cetartiodactyla. Journal of Paleontology 78:39–44.
- Thomas, C.D., W.e Kunin. 1999. The spatial structure of populations. Journal of Applied Ecology 68:647-657.
- Thomas, M.G., E. Hagelberg, H.B. Jones, Z. Yang, A.M. Lister. 2000. Molecular and morphological evidence on the phylogeny of the Elephantidae. Proceedings of the Royal Society London B 267:2493-2500.
- Tjørve, E. 2003. Shapes and functions of species–area curves: a review of possible models. Journal of Biogeography 30:827–835.
- Tokeshi, M. 1992. Dynamics and distribution in animal communities: theory and analysis. Research in Population Ecology 34:249-273.
- Tonn, W.M., J.J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. Ecology 63:1149-1166.
- Triantis, K.A., D. Nogues-Bravo, J. Hortal, Borges PAV, H. Adsersen, J. M. Fernandez-Palacios, M. B. Araujo, R. J. Whittaker. 2008. Measurements of area and the (island) species-area relationship: new directions for an old pattern. Oikos 117:1555-1559.
- Triantis, K.A., M. Mylonas, K. Lika, K. Vardinoyannis. 2003. A model for the species-area-habitat relationship. Journal of Biogeography 30:19–27.
- Tsubamoto, T., M. Takai, N. Egi. 2004. Quantitative analyses of biogeography an faunal evolution of middle to late Eocene mammals in East Asia. Journal of Vertebrate Paleontology **24**:657–667.
- Uhlenbeck, G.E., L.S. Ornstein. 1930. On the theory of Brownian Motion. Phys.Rev. 36:823–41.
- Valentine, J.W., K. Roy, D. Jablonsky. 2002. Carnivore/non-carnivore ratios in northeastern Pacific marine gastropods. Marine Ecology. Progress Series 228:153–163.
- Van Valen, L. 1973. A new evolutionary law. Evol. Theory 1:1-30.

- Van Valkenburgh, B. 1988. Trophic diversity in past and present guilds of large predatory mammals. Paleobiology 14:155–173.
- Van Valkenburgh, B., C.M. Janis. 1993. Historical diversity patterns in North American Large herbivores and carnivores. Pp. 330-340 *in* Ricklefs, R.E., Schluter, D. eds. Species Diversity in Ecological Communities. The University of Chicago Press, Chicago.
- Venable, D.L., J.S. Brown. 1993. The Population-Dynamic Functions Of Seed Dispersal. Vegetatio 108:31-55.
- Vezina, A., 1985. Empirical relationship between predator and prey size among terrestrial vertebrate predators. Oecologia 67:555–565.
- Vrba, E.S. 1995a. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: ES Vrba, GH Denton, TC Partridge and LH Burckle (eds) Paleoclimate And Evolution With Emphasis On Human Origins, Yale Univ. Press, New Haven And London, pp. 385–424.
- Vrba, E.S., 1995b. On the connections between paleoclimate and evolution. Pp. 24-48 *in* Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. eds. Paleoclimate and Evolution With Emphasis on Human Origins. Yale Univ. Press, New Haven and London.
- Vrba, E.S., D. deGusta. 2004. Do species populations really start small? New perspectives from the Late Neogene fossil record of African mammals. Philosophical Transaction of the Royal Society B 359:285–292.
- Waddell, P., N. Okada, M. Hasegawa. 1999. Towards resolving the interordinal relationships of placental mammals. Systematic Biology 48:1–5.
- Waldron, A. 2007. Null models of geographic range size evolution reaffirm its heritability. The American Naturalist 170:221–231.
- Walsh, S.L. 1998. Fossil datum terms, paleobiological event terms, paleontostratigraphy, chronostratigraphy, and the definition of land-mammal “age” boundaries. Journal of Vertebrate Paleontology 18:150–179.
- Wang, X., R.H. Tedford, B. Van Valkenburgh, R.K. Wayne. 2004. Phylogeny, Classification, and Evolutionary Ecology of the Canidae. *In* C. Sillero Zubiri, C. Hoffmann, D. W. Macdonald eds. Canids:Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan. IUCN/SSC Canid Specialist Group.

- Warren, P.H., K.J. Gaston, 1992. Predator–prey ratios: a special case of a general pattern? Phil. Trans. R Soc. Lond. Ser. B Biol. Sci. 338:113–130.
- Webb, T.J., K.J. Gaston, K. 2000. Geographic range size and evolutionary age in birds. Proceedings of the Royal Society. B 267:1843–1850.
- Webb, T.J., K.J. Gaston, K. 2003. On the heritability of geographic range sizes. The American Naturalist 161:553–566.
- Webster, A.J., A. Purvis. 2002. Testing the accuracy of methods for reconstructing ancestral states of continuous characters. Proceedings of the Royal Society of London Series B-Biological Sciences 269(1487):143-149.
- Werdelin, L., N. Solounias. 1991. The Hyaenidae: taxonomy, systematics and evolution. Fossils and Strata 30:1-104.
- West G.B., J.H. Brown, B.J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology Science 276:122-126.
- White, E.P. 2004. Two-phase species-time relationships in North American land birds. Ecology Lett 7:329-336.
- White, E.P. 2007. Spatiotemporal scaling of species richness: patterns, processes, and implications. P.P 325-346 *in* Storch D., P.A. Marquet, J.H. Brown, eds. Scaling Biodiversity. Cambridge University Press.
- White, E.P., P.B. Adler, W.K. Lauenroth, R.A. Gill, D. Greenberg, D.M. Kaufman, A. Rassweiler, J. A. Rusak, M. D. Smith, J. R. Steinbeck, R. B. Waide, J. Yao. 2006. A comparison of the species-time relationship across ecosystems and taxonomic groups. Oikos 112:185-195.
- Whittaker, R.J. 1998. Island Biogeography. Oxford University Press, Oxford.
- Whittaker, R.M. 1972. Evolution and measurement of species diversity. Taxon 21:213-251.
- Williams, C.B. 1943. Area and the number of species. Nature 152:264-267.
- Williams, C.B. 1964. Patterns in the Balance of Nature. Academic Press, London.
- Williams, H.S. 1901. The discriminating of time-values in geology. Journal of Geology 9(7):570-585.
- Williamson, M.H. 1981. Island Populations. Oxford University Press, Oxford.
- Williamson, M.H. 1988. Relationship of species number to area, distance and other variables. Pp.91-15 *in* Myers, A.A.P.S. Giller eds. Analytical biogeography,

an integrated approach to the study of animal and plant distributions. Chapman and Hall.

- Wood, H.E., R.W. Chaney, J. Clark, E.H. Colbert, G.L. Jepson, J.B. Reedside, C. Stock. 1941. Nomenclature and correlation of the North American continental Tertiary. Geological Society of America Bulletin 52:1–48.
- Woodburne, M.O., C.C. Swisher III. 1995. Land mammal high resolution geochronology, intercontinental overland dispersals, sea-level, climate, and vicariance. Pp. 335-364 *in* W. A. Berggren, D. V. Kent, and J. Hardenbol eds. Geochronology, time-scales and global stratigraphic correlation: framework for an historical geology. Society of Stratigraphic Geology, Special Publication 54.
- Wrigth, D.H. 1983. Species-energy theory: an extension of species area theory. Oikos 41:496-506.
- Wyle, J.L., D.J. Currie. 1993. Species-energy theory and patterns of species richness: I.Patterns of bird, angiosperm, and mammal species richness on island. Biological Conservation 63:137-144.
- Zachos J., M. Pagani, L. Sloan, E. Thomas, K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686-693.
- Zar, J.H. 1984. Biostatistical Analysis. 2nd eds. Prentice Hall, Englewood Cliffs, New Jersey.

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